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THE UNIVERSITY OF ALBERTA

The effect of salt concentration on ecological and physiological aspects of growth of *Distichlis stricta*

by

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A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE
IN
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Lawrence C. Bliss

Supervisor

Doug Whitfield

James M. Mayo

J. R. Webster

Date November 28, 1979

To *Recurvirostra americana*, summer resident
of Akasu Lake.

Abstract

Distichlis stricta (saltgrass) a common species of inland alkaline soils, was the subject of descriptive and experimental ecophysiological studies.

A relatively undisturbed saltgrass community near Vegreville, Alberta was selected as a field site. A gradient of plant size was found at this site. Soils under the two extremes (short and tall saltgrass) were compared for clues to the cause of the height difference.

Chemical analyses of soil extracts showed few differences between the two soils. Both had high pH (typically 8.3), high electrical conductivities (35 mS/cm), high total cation (TC) concentrations (400 to 500 me/l), high magnesium (140 me/l) and sodium (300 me/l) concentrations, low calcium (25 me/l) and potassium (3 me/l) concentrations, and high Mg/Ca ratios (5). Measurements taken over several months revealed that soil temperatures were higher and soil moisture levels lower in the short than in the tall saltgrass zone. In contrast with the findings of other studies, results at this site indicated that these soil physical properties were more limiting to saltgrass growth than soil chemical characteristics.

Community analyses showed that there was low plant cover and low species diversity in the saltgrass communities. *Hordeum jubatum*, *Puccinellia nuttalliana*, and *Suaeda calceoliformis* were the species most consistently associated with *D. stricta*.

Controlled environment experiments with saltgrass growth used nutrient solutions based on cation concentrations and ratios found in soil solutions at the field site. Plants grown at different cation ratios and concentrations (from 0 to 368 me/l TC) showed no significant differences in growth form or biomass. They did have some significantly different internal ion concentrations related to solution differences, but tissue ion levels appeared to be regulated such that they fell within a range suitable for growth. Shoot calcium concentrations were relatively low (0.07 - 0.35 me/g). Ca/TC ratios did not seem to be crucial for this species: plants remained healthy even when the tissue Ca/TC ratio dropped below 0.10. Tissue magnesium and sodium levels were kept low (0.16 - 0.31 and 0.04 - 0.57 me/g respectively) by exclusion and/or excretion of these ions. Potassium concentrations were always relatively high (0.35 - 0.65 me/g), probably due to active uptake. Shoot K/TC ratios were also very high (up to 0.50 in some cases), showing that potassium was the preferred monovalent cation. There were no significant differences in total cation concentrations in tissue of plants grown in solutions with low to high salt concentrations: TC was almost always between 0.8 and 1.2 me/g.

Saltgrass plants grown in solutions with different osmotic potentials were always able to maintain a water potential gradient between shoots and solution. The lowest water potential reached was -1252 KPa for plants grown in a

solution with an osmotic potential of -970 kPa. Osmotic adjustment may have been due to potassium accumulation and/or production of organic solutes. Saltgrass grew very well in solution with no added sodium. This species apparently does not require sodium for good growth, and is able to survive in saline environments by excluding or excreting sodium and magnesium.

Germination of saltgrass seeds in four salt solutions was delayed and decreased by low osmotic potentials. Maximum germination (51%) occurred at 0 or -200 kPa; there was no germination at -2000 kPa. Sodium chloride and sulfate were least inhibitory, and magnesium sulfate and PEG most inhibitory to germination.

Preface

"About 97% of the total water supply of the world is in the oceans. The concentration of NaCl in this water is almost 0.5 M. The energy input which powers the life in the ocean is entirely through the activities of photosynthetic plants, the phytoplankton. These plants are adapted for life in this saline environment.

Oceanic plants are not the only ones fitted for life under highly saline conditions. The shores of the oceans and the salt marshes and saline deserts of the world are the habitats of green plants which possess the same competence (halophytes). By way of marked contrast, most of the species of crop plants on which we rely for food cannot tolerate solutions in their root medium having a salinity higher than about 10 to 20% of that of sea water and many fail at even lower salinity.

Taken together, these facts present a challenge and an opportunity. There is no basic incompatibility between plant life and saline conditions. The oceanic flora and the terrestrial halophytes attest to that. We are, however, ignorant of the physiological and metabolic devices which enable these plants to thrive under saline conditions fatal to most crop plants. Comparative studies are therefore called for concerning the salt relations of salt-sensitive and salt-tolerant plants, in order to enable us to understand and eventually, to manipulate and control, the mechanisms making for salt tolerance."

Elzam, O. E. and E. Epstein. 1969. Agrochimica 13: 187.

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I would like to thank my supervisor, Dr. L. C. Bliss, for his assistance in choosing this project and for his advice and encouragement along the way. Thanks are also due my committee members for their helpful comments on the research project and thesis. I especially thank Dr. J. M. Mayo for his practical guidance and boundless enthusiam.

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Mr. M. Juba was kind enough to permit me to set up equipment, carry out my field study, and watch birds on his land near Vegreville, Alberta. Thanks to the Vegreville Bakery for making poppy seed buns which fueled my fieldwork.

My longtime (and long-suffering) field assistant Beth Honeybunch was responsible for much of the data collection at the field site, and her cheerful help is greatly appreciated.

I especially thank Dave Cuthiell for his tangible assistance and unwavering moral support which helped me to persevere in this endeavor. In particular, I thank him for introducing me to the avifauna of Alberta, for helping me to unstick my car from the treacherous Vegreville clays, and for accompanying me on a pick-wielding expedition to my field site in the dead of winter to collect rhizomes.

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Table of Contents

Chapter Page

1. INTRODUCTION 1

2. LITERATURE REVIEW 5

  2.1 The Physical Environment of Halophyte Communities .. 5

    2.1.1 Meteorological conditions 5

    2.1.2 Soils of halophyte communities 7

      2.1.2.1 Terminology 7

      2.1.2.2 Formation of saline soils 8

      2.1.2.3 Physical characteristics of saline soils 10

      2.1.2.4 Chemical characteristics of saline soils 11

  2.2 Relationships of Species in Halophyte Communities . 14

    2.2.1 Species associated with *Distichlis stricta* .. 14

    2.2.2 Species zonation with respect to soil conditions 15

    2.2.3 Vegetational analysis 16

  2.3 Halophyte Phenology 17

  2.4 Growth of Plants in Solution Culture With Added Salts 19

    2.4.1 Use of solution culture 19

    2.4.2 Importance of cations in plant growth 20

    2.4.3 Cation uptake from soil and culture solutions 26

    2.4.4 Osmotic and specific effects of added salts . 31

    2.4.5 Water relations of plants grown with added salts 32

  2.5 Germination 36

    2.5.1 Osmotic effects 36

2.5.2 Specific effects 38

2.5.3 Recovery of germination ability 38

3. MATERIALS AND METHODS 40

3.1 The Physical Environment 40

3.1.1 Location of field study site 40

3.1.2 Meteorological data 40

3.1.3 Soil physical measurements 43

3.1.4 Soil chemical analyses 43

3.2 Community Characterization 47

3.2.1 Description of species present 47

3.2.2 Community sampling system 48

3.2.3 Saltgrass zone transects 50

3.3 Growth of Distichlis stricta in the Field 50

3.3.1 Phenological observations 50

3.3.2 Shoot growth 50

3.3.3 Flowering percentage 51

3.4 Solution Culture Studies 51

3.4.1 Experiment 1 51

3.4.1.1 Experimental design 52

3.4.1.2 Preparation of plants 54

3.4.1.3 Harvesting and tissue analyses 58

3.4.1.4 Statistical analyses 58

3.4.2 Experiment 2 59

3.4.2.1 Experimental design 59

3.4.2.2 Preparation of plants 62

3.4.2.3 Water potential measurements 64

3.4.2.4 Harvesting and tissue analyses 66

3.4.2.5 Statistical analyses 66
3.5 Germination 67
3.5.1 Experimental design 67
3.5.2 Preparation of solutions and seeds 68
3.5.3 Recovery of germination ability 69
3.5.4 Statistical analyses 70
4. RESULTS 71
4.1 The Physical Environment 71
4.1.1 Micrometeorological data 71
4.1.2 Soil physical measurements 71
4.1.3 Soil chemical analyses 75
4.2 Community Characterization 93
4.2.1 Description of species present 93
4.2.2 Community sampling 93
4.2.3 Saltgrass zone transects 99
4.3 Growth of saltgrass in the field 102
4.3.1 Phenological observations 102
4.3.2 Shoot growth 102
4.3.3 Flowering percentage 104
4.4 Solution Culture Studies 104
4.4.1 Experiment 1 104
4.4.1.1 Growth of plants 104
4.4.1.2 Tissue analyses 108
4.4.2 Experiment 2 118
4.4.2.1 Growth of plants 118
4.4.2.2 Water potential measurements 121
4.4.2.3 Tissue analyses 124

4.5 Germination 138
    4.5.1 Germination of seeds in osmotica 138
    4.5.2 Recovery of germination ability 140
5. DISCUSSION 143
  5.1 The Physical Environment 143
    5.1.1 Micrometeorological data 143
    5.1.2 Soil physical measurements 143
    5.1.3 Soil chemical analyses 144
  5.2 Community Characterization 151
    5.2.1 Description of species present 151
    5.2.2 Community sampling 152
    5.2.3 Saltgrass zone transects 154
  5.3 Growth of Saltgrass in the Field 155
    5.3.1 Phenological observations 155
    5.3.2 Growth of tagged shoots 155
    5.3.3 Flowering percentage 156
  5.4 Solution Culture Studies 157
    5.4.1 Experiment 1 157
      5.4.1.1 Growth of plants 157
      5.4.1.2 Tissue analyses 158
    5.4.2 Experiment 2 164
      5.4.2.1 Growth of plants 164
      5.4.2.2 Water potential measurements 167
      5.4.2.3 Tissue analyses 170
    5.4.3 Survival strategy of saltgrass 178
  5.5 Germination 180
6. CONCLUSIONS 183

REFERENCES..188

APPENDICES ABBREVIATIONS................................205

APPENDIX 1. T-test comparison of shoot height of tall and short saltgrass plants..............................206

APPENDIX 2. Short and tall saltgrass flowering percentages; raw data and t-test comparison of means.207

APPENDIX 3. Experiment 1 growth variables; raw data and one-way analyses of variance...........................209

APPENDIX 4. Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions..212

APPENDIX 5. Experiment 1 cation ratios; raw data, one-way analyses of variance, and linear regressions.219

APPENDIX 6. Experiment 1 correlations of dry weight with cation concentrations and ratios.....................226

APPENDIX 7. Experiment 2 growth variables; raw data, one-way and two-way analyses of variance.............227

APPENDIX 8. Barley (*Hordeum vulgare*) raw data, Experiment 2..231

APPENDIX 9. Experiment 2 pressure bomb raw data, one-way analysis of variance, and correlation test...........232

APPENDIX 10. Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.......233

APPENDIX 11. Experiment 2 cation ratios; raw data, two-way and one-way analyses of variance.............240

APPENDIX 12. Experiment 2 correlations of dry weight with cation concentrations and ratios................247

APPENDIX 13. Germination raw data, two-way and one-way analyses of variance...................................248

List of Tables

Table 1. Composition of nutrient solutions used in Experiment 1..........53

Table 2. Composition of nutrient solutions used in Experiment 2..........60

Table 3. Temperature extremes at Akasu Lake, summer 1978..73

Table 4. Soil temperatures of three saltgrass zones at Akasu Lake, 1978..........74

Table 5. Chemical analyses of 1978 water samples from Akasu Lake..........92

Table 6. Species in or near the *Distichlis stricta* community at Akasu Lake..........94

Table 7. Cover classes of species in sampling area #1 at Akasu Lake..........96

Table 8. Cover classes of species in sampling area #2 at Akasu Lake..........97

Table 9. Frequency of species in two sampling areas at Akasu Lake..........98

Table 10. Flowering percentages of short and tall *Distichlis stricta* in 1977 and 1978..........105

Table 11. Saltgrass growth data for solution culture Experiment 1..........107

Table 12. Saltgrass growth data for solution culture Experiment 2..........122

Table 13. Recovery of germination ability by osmotically stressed saltgrass seeds..........141

Table 14. Physical and chemical characteristics of surface soils under saltgrass stands..........145

Table 15. Cation concentrations and percent salts of surface soils under saltgrass stands..........146

Table 16. Cation ratios of surface soils under saltgrass stands..........147

Table 17. Calcium and magnesium concentration ranges in shoots of various plant species grown at constant or uncontrolled salinity levels..........161

Table 18. Sodium and potassium concentration ranges in shoots of various plant species grown at constant or uncontrolled salinity levels..........................162

Table 19. Calcium and magnesium concentration ranges in shoots of various plant species grown at increasing salinity levels....................................175

Table 20. Sodium and potassium concentration ranges in shoots of various plant species grown at increasing salinity levels....................................176

List of Figures

Figure 1. Male and female plants of *Distichlis stricta*.....4

Figure 2. Location of study site at Akasu Lake............41

Figure 3. Sampling areas and transects in saltgrass community at Akasu Lake...............................44

Figure 4. Detail of 32 m by 32 m cross-shaped sampling area...49

Figure 5. Placing of plants in container, solution culture Experiment 1 56

Figure 6. Cutaway view of container with plants, solution culture Experiment 2 65

Figure 7. Summary of air temperatures at 10 cm at Akasu Lake site, summer 1978 72

Figure 8. Percent soil moisture (Pw) of soil samples from three saltgrass zones 76

Figure 9. Saturation percentages of soil samples from three saltgrass zones 77

Figure 10. Saturation paste pH readings of soil samples from three saltgrass zones 78

Figure 11. Electrical conductivity of saturation extracts (ECe) from soils of three saltgrass zones ...79

Figure 12. Calcium concentration of saturation extracts from soils of three saltgrass zones 80

Figure 13. Magnesium concentration of saturation extracts from soils of three saltgrass zones 81

Figure 14. Sodium concentration of saturation extracts from soils of three saltgrass zones 82

Figure 15. Potassium concentration of saturation extracts from soils of three saltgrass zones 83

Figure 16. Total cation concentration of saturation extracts from soils of three saltgrass zones 84

Figure 17. Magnesium to calcium ratio of saturation extracts from soils of three saltgrass zones 86

Figure 18. Cation to total cation concentration ratios of saturation extracts from soil of short Ds zone.....87

Figure 19. Cation to total cation concentration ratios of saturation extracts from soil of tall Ds zone......88

Figure 20. Cation to total cation concentration ratios of saturation extracts from soil of tall, scattered Ds zone..89

Figure 21. Sodium adsorption ratio (SAR) of saturation extracts from soils of three saltgrass zones 91

Figure 22. Shore to shore transect through *Distichlis stricta* community at Akasu Lake.....................95

Figure 23. Percent cover of species along Transect 1.....100

Figure 24. Percent cover of species along Transect 2.....101

Figure 25. Growth of tagged saltgrass shoots and corresponding soil moisture levels at Akasu Lake 103

Figure 26. Mean calcium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1) 109

Figure 27. Mean magnesium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1) 110

Figure 28. Mean sodium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1) 112

Figure 29. Mean potassium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1) 113

Figure 30. Mean total cation concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1) 114

Figure 31. Mean tissue Mg/Ca vs. solution Mg/Ca ratio for saltgrass grown at four levels of Mg/Ca (Experiment 1) 115

Figure 32. Cation to total cation concentration ratios in tissue vs. solutions for saltgrass grown at four levels of Mg/Ca (Experiment 1).......................116

Figure 33. Mean water potential of saltgrass shoots grown at various Mg/Ca ratios and salt concentrations (Experiment 2).......................123

Figure 34. Mean calcium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2) 125

Figure 35. Mean magnesium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2) 127

Figure 36. Mean sodium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2) 128

Figure 37. Mean potassium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2) 129

Figure 38. Mean total cation concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2) 131

Figure 39. Mean Mg/Ca ratios in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2) 132

Figure 40. Cation to total cation concentration ratios in solutions C to B3 of Experiment 2 134

Figure 41. Cation to total cation concentration ratios in saltgrass grown at various Mg/Ca ratios and salt concentrations 135

Figure 42. Mean percent germination of saltgrass seeds placed in four osmotica 139

List of Plates

Plate 1. Saltgrass field study site at Akasu Lake, Alberta 42

Plate 2. Pot set-up in growth chamber, Experiment 1 57

Plate 3. Collection of short *Distichlis stricta* plants from frozen soil 63

Plate 4. Effect of increasing Mg/Ca and decreasing Ca/TC on growth of saltgrass in Experiment 1 106

Plate 5. Growth of saltgrass at two weeks in Experiment 2 119

Plate 6. Growth of saltgrass at eight weeks in Experiment 2 120

List of Abbreviations

Ds	*Distichlis stricta*, saltgrass
HG	hygrothermograph
Pw	percent soil moisture
SP	saturation percentage
EC	electrical conductivity in mS/cm at 25 C (1 mS/cm = 1 mmho/cm)
ECe	electrical conductivity of soil saturation extract, mS/cm at 25 C
TC	total cation concentration, Ca + Mg + Na + K unless otherwise specified
μ	ionic strength, moles/liter
ANOV	analysis of variance
p	probability
SAR	sodium adsorption ratio
PEG	polyethylene glycol
SEM	standard error of mean
OP	osmotic potential

1. INTRODUCTION

Sodium salts strongly influence the lives of many marine and terrestrial organisms. The ability of certain plant species to complete their life cycles in highly saline environments has long been of interest to botanists. With the spread of salinity in soils of arid regions becoming an ever increasing problem, the use of native salt adapted species in reclamation, and the development of salt tolerant crop species, appear to be major parts of the solution.

Plants which consistently and specifically complete their life cycles in habitats having high salt concentrations are called halophytes (Waisel 1972). Halophyte species usually have wide distributions which are controlled mainly by edaphic factors. Halophyte communities of inland North America are widely scattered, occurring wherever a combination of moisture and salts has led to the development of saline soils. Species present in these communities are able to withstand conditions which most plant species cannot tolerate.

While a great deal of research has been done on the effects of salinity on agricultural plants, less has been done with halophytes. Halophyte survival strategies, which may involve avoidance or tolerance of high tissue salt concentrations, are not fully understood.

The objective of this project was to investigate the survival strategy of *Distichlis stricta* (Torr.) Rydb. (saltgrass) by studying some ecological and physiological aspects of its life cycle. These were the following: 1) microclimatic and edaphic factors involved in growth and local distribution, 2) relationships with other species, 3) pattern of growth in the field, 4) survival, water relations and internal cation relations in controlled nutrient solutions, and 5) germination of seeds in various media with decreasing osmotic potentials.

While there is a substantial amount of information available regarding the community relations of *Distichlis stricta*, there has been less research done regarding the physiological aspects of its tolerance to saline conditions, especially under laboratory conditions. Osmotic pressures of leaves and stems of *D. stricta* from a saline meadow in Saskatchewan were measured by Dodd and Coupland (1966a). Detling (1969) measured photosynthetic and respiratory rates and water potentials of four halophytes in Utah including *D. stricta* . Tiku (1976) recorded growth, photosynthetic rates, and tissue osmotic potentials of saltgrass grown in solutions of decreasing osmotic potential. Hansen et al. (1976) quantified edaphic factors, tissue contents and salt gland activity, and carried out scanning electron microscopy on *D. stricta* plants from Utah. Nielson (1956) studied variability in several factors, including germination, of *D. stricta* collected from several areas in the western United States.

Since saltgrass communities are fairly common in Alberta, and since little of the previous work combined ecological and physiological studies, it was felt that this would be an excellent species on which to base a more comprehensive investigation of salinity effects on halophyte growth.

Distichlis stricta is found from British Columbia to Saskatchewan and south to Arizona and New Mexico (Fassett 1925, Ungar 1974b). Examination of many *Distichlis* collections led Fassett (1925) to conclude that the species is extremely variable in size, habit and technical characters. Saltgrass (Figure 1) is a perennial, dioecious grass with extensive creeping rhizomes, sharp tipped leaves from 5 to 12 cm long, and panicles with several crowded flat spikelets (Moss 1959). Active salt glands are found on both leaf surfaces (Hansen et al. 1976). In soils of low to moderate salinity, the plants are relatively tall and robust, while at higher salinities a short or dwarf growth form is usually found.

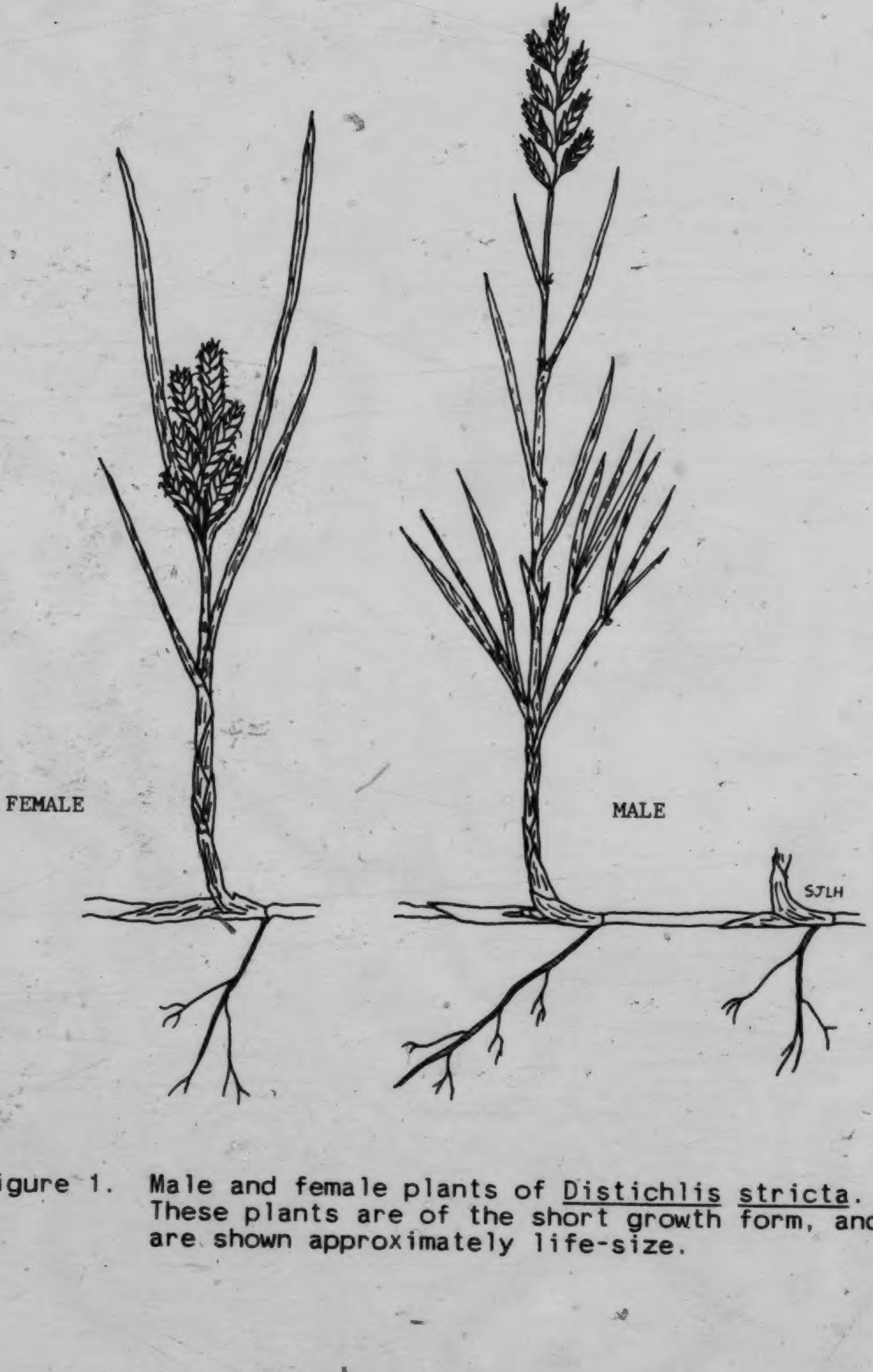

FEMALE
MALE
SJLH

Figure 1. Male and female plants of Distichlis stricta. These plants are of the short growth form, and are shown approximately life-size.

2. LITERATURE REVIEW

2.1 The Physical Environment of Halophyte Communities

2.1.1 Meteorological conditions

Inland halophyte communities are found from desert areas of the United States (Billings 1945, Hunt and Durrell 1966) to areas of Solonetzic soils located within the boreal forest region of northern Alberta (Reeder and Odynsky 1964). Some halophyte species, including *Distichlis stricta*, are found over the entire range. These species must withstand a wide range of climatic conditions. Hunt and Durrell (1966) reported that in Death Valley, California where saltgrass is found around the edge of the saltpan, summer temperatures may reach as high as 57 C. The average July temperature is 38 C. Frosts are rare, as is rainfall which averages about 4 cm annually on the valley floor. Relative humidity is frequently 5 to 15% in summer.

Halophyte communities in Oklahoma, Kansas, and Nebraska experience less extreme climatic conditions than those in the deserts. Annual precipitation in these areas averages 46 to 66 cm, with about 75% falling during the 180 to 210 day growing season (Tolstead 1942, Ungar 1967, 1968). The mean annual temperature in northern Oklahoma, where *Distichlis stricta* is found on the Great Salt Plains, is 16 C, while the mean temperature of the warmest month (July) is 29 C (Ungar 1968). In Colorado, where halophytes grow at 2900 m, the temperatures are considerably lower (mean annual temperature is 4 C, July mean is 15 C) and annual precipitation is only 27 cm (Ungar 1974a). *Distichlis stricta* and other halophytes are also found growing at spring fed salt marshes in western Utah where only 13% of the 18 cm of annual precipitation falls during the summer months (Bolen 1964).

In North and South Dakota, where halophyte communities are widespread, annual precipitation averages 44 to 52 cm with 70 to 80% falling during the 125 to 130 day growing season. Mean annual temperature ranges from 4 to 6 C, and July mean temperature averages 20 to 22 C (Dix and Smeins 1967, Ungar 1970, Redmann 1972). The climate of southern Saskatchewan where saline lakes are common is characterized by low humidity, high winds, mean annual precipitation of 30 to 40 cm (with 70% falling as rain during the growing season), mean annual temperature of 1 C, and July mean temperature of 19 C (Rawson and Moore 1944, Dodd and Coupland 1966b).

In Alberta, *Distichlis stricta* has been found growing on salt flats at Fort Vermilion, and in Wood Buffalo National Park at 60 degrees north latitude (University of Alberta Herbarium Records). Halophytes growing in this region experience a climate far removed from that of the previously described desert areas. Meteorological records of 30 years at Fort Vermilion indicate that the mean annual temperature is -1 C, while mean July temperature is 16 C (Alberta Environment 1976). Extreme temperatures of 39 and

-60 C have been recorded. The annual precipitation is about 36 cm, with half falling from May to September. The mean duration of the summer frost-free period is only 65 days (Kendrew and Currie 1955).

The above discussion of the wide range of climatic conditions in which halophytes occur suggests that other factors must control distribution of these species. Edaphic factors are of primary importance in this regard, since in most cases halophyte species are limited to saline soils on which few other species can survive.

2.1.2 Soils of halophyte communities

2.1.2.1 Terminology

The U.S. Salinity Laboratory first proposed a classification of salt affected soils based on ECe (electrical conductivity of saturation extracts), ESP (exchangeable sodium percentage), and SAR (sodium adsorption ratio) (Richards 1954). A saline soil is characterized by an ECe greater than 4 mS/cm at 25 C, an ESP less than 15, and pH less than 8.5. These soils are flocculated and have high permeability, but they contain sufficient soluble salts to reduce crop growth. Nonsaline alkali (sodic) soils have an ESP or SAR greater than 15, an ECe less than 4, and a pH of 8.5 to 10. Crop growth in these soils may be severely impaired due to soil dispersion and subsequent decreased permeability, and nutritional disorders caused by high pH. Saline alkali (saline sodic) soils have an ECe greater than

4, ESP or SAR greater than 15, and pH usually less than 8.5. Since excess salts are present, the physical properties of these soils are similar to those of saline soils. Abrol and Bhumbla (1978) suggested that classifying both saline and saline sodic soils as saline would be more appropriate for the following reasons: very few true saline soils exist, salinity effects are more important than sodicity effects in saline sodic soils, and the physical properties of the two types are very similar. The term saline will be used to describe soils of halophyte communities in this thesis.

2.1.2.2 Formation of saline soils

Saline soils are intrazonal, that is they occur in a wide range of zones intermixed with normal nonsaline soils. Their formation is dependent upon deposits of marine bedrock, weathering of soil minerals, the presence of high water tables, and evaporation (Kelley 1951). Saline soils are generally found in discharge areas -- areas which are or at one time were characterized by a high water table caused by movement of groundwater from higher recharge areas (Nielsen 1973). Extreme discharge areas may have springs, quick ground or sloughs, while others with lower discharge rates may have well developed saline soils covered with salt tolerant vegetation (Nielsen 1973).

Precipitation with dissolved carbon dioxide infiltrates the soil at a recharge area, forming weak carbonic acid which dissolves soil minerals as it percolates downward to the groundwater level (Nielsen 1973). Groundwater flows over a less permeable layer to the discharge area, dissolving salts from soil and bedrock as it moves. In the Northern Great Plains region the bedrock in many areas is marine in origin, and the glacial and postglacial materials derived from the bedrock are rich in salts (Vander Pluym 1978). If movement of the groundwater through soil and bedrock is slow, the concentration of dissolved salts increases.

Salinization of soil at the discharge area usually results in a flocculated, permeable soil which may be leached to form a Solonetzic soil, or may remain saline due to repeated discharge of saline groundwater (Clayton et al. 1977). The processes involved in formation of soils of the Solonetzic order are described by Cairns and Bowser (1977) and Clayton et al. (1977). Salinization is followed by removal of salts by precipitation, provided that there is a drop in the water table. If enough sodium is present, clay and organic matter deflocculate and are carried down to the B horizon where they form a compact nearly impermeable layer. At this point the soil is a Solonetz. If leaching continues, solodization takes place. The platy A horizon becomes thicker, and the Solonetzic B horizon begins to break down, so that a transitional AB horizon forms. The soil is then a solodized Solonetz which can support the growth of moderately salt tolerant species.

In arid regions of North America, saline soils can form wherever evaporation exceeds total precipitation (Kelley 1951). In these areas, precipitation dissolves soil minerals but does not move them out of the profile. They accumulate and rise to the surface where they are concentrated by evaporation.

2.1.2.3 Physical characteristics of saline soils

The physical characteristics of saline soils depend primarily on the concentration and proportions of dissolved ions on the exchange complex and in the soil solution. In saline soils where total salt concentration is relatively low but ESP is relatively high, repulsion of the diffuse double layers of adjacent clay particles may cause dispersion of soil particles (Russell 1973). Dispersion decreases the size of the large soil pores and reduces hydraulic conductivity (Shainberg 1975). Studies of Solonetzic soils in western Canada have shown that the characteristic Bn horizons may have hydraulic conductivity values of zero (Bowser et al. 1962). Water movement into the A horizons may also be very slow, leading to surface evaporation and runoff (Cairns and van Schaik 1968).

When there is an excess of salts present in the soil, flocculation of soil particles occurs and hydraulic conductivity is much higher than in dispersed soils (Shainberg 1975). Flocculated soils tend to have good structural characteristics, allowing for easy water and root penetration, and good aeration.

Soil moisture availability is generally not a problem in discharge areas where the water table is close to the surface. In arid regions where the water table is deep and precipitation scarce, halophytes must develop extensive root systems to maintain contact with available water (Hunt and Durrell 1966).

2.1.2.4 Chemical characteristics of saline soils

Saline soils are characterized by medium to high pH, high ECe, high cation concentrations, and high SAR (Richards 1954). The presence of high concentrations of sodium and/or magnesium generally results in cation ratios which are adverse compared with those found in normal soils.

The pH of saline soils is usually basic, although the upper horizons of well developed Solonetzic soils may be quite acidic due to leaching of clay and organic matter (Cairns 1961). The pH found in the upper horizons of saline soils on which *Distichlis stricta* grows may range from 7 to 10, with a median of about 8 (Bolen 1964, Ungar 1967, 1974b, Hansen et al. 1976). This wide range of pH indicates that species distribution and soil pH are not closely correlated (Ungar 1968, 1970, 1974a). Although soil pH can affect the solubility of nutrients (Shainberg 1975), the pH variations found in soils of halophyte communities do not seem to significantly affect species growth and distribution.

Extracts of soils under halophyte communities generally have high electrical conductivities. For example, the ECe of soils under tall saltgrass may range from 7 to 24 mS/cm, while for soils under the short growth form, ECe ranges from 19 to as high as 104 (Ungar 1967, 1968, 1970). Solonetzic soils, which have undergone at least some leaching of salts, have lower conductivities than those just described. The ECe of A horizons may range from 1 to 5, and of B horizons from 2 to 12 mS/cm (Cairns 1961). There are seasonal variations in ECe of saline soils, with the highest values generally occurring in the warmest and driest months.

Some cation concentrations in the soil solution and on the exchange complex of saline soils are many times higher than those of corresponding nonsaline soils. Sodium is usually the dominant cation, although in some areas magnesium may also occur in high concentrations (Cairns 1961, Dodd et al. 1964). Calcium concentrations tend to be much lower than sodium concentrations, but higher than potassium concentrations (Bowser et al. 1962, Ungar 1974a). The dominant anion may be sulfate or chloride, depending on the source of the salts (Ungar 1974b). Total salt concentrations found under saltgrass communities may be as low as 0.13% (Ungar 1966) or as high as 4.2% under the short growth form (Ungar et al. 1969).

Ion concentrations and ratios in saline soils are dependent upon soil moisture levels. As soil moisture increases due to precipitation, or decreases due to evaporation, ion concentrations in the soil solution increase or decrease respectively. However, the soil moisture-ion concentration relationship is not simply one of inverse proportion (for example, see Moss 1963), and can be different for different soils (Carter 1977). Khan and Webster (1966) found that at the low range of moisture content of a Solonetzic soil, increasing moisture caused abrupt changes in ion ratios, while at the higher moisture range, changes were less dramatic. They suggested that at the low moisture levels a three phase equilibrium may be present between excess solid salts, soil particles, and the soil solution, while at higher moisture contents, soil particles and soil solution are the main phases.

Few saline soils of halophyte communities have been analyzed as thoroughly as salt affected agricultural soils, so there is little specific information on cation ratios found in undisturbed saline soils. It is to be expected that the dominance of sodium and sometimes magnesium in these soils results in low calcium to total cation ratios, high magnesium to calcium ratios, and low potassium to total cation ratios. These conditions would reduce or prevent the growth of most agricultural species, but are readily tolerated by many halophytes.

High salt concentrations cause low soil osmotic potentials, making water uptake by plants difficult. This factor is one of the most important in controlling plant distribution in halophyte communities (Ungar et al. 1969, Ungar 1970, 1974a, Ungar et al. 1979). Halophyte species usually occupy characteristic locations with respect to total salinity and soil moisture (Ungar 1974a), making them useful as indicators of soil conditions (Richards 1954).

2.2 Relationships of Species in Halophyte Communities

2.2.1 Species associated with *Distichlis stricta*

Many authors have noted the remarkable ability of *Distichlis stricta* to withstand a very wide range of soil conditions, and consequently to grow with a great variety of plant species (Shantz and Piemeisel 1924, Flowers 1934, Billings 1945, Dodd and Coupland 1966b, Ungar 1967b, 1970, 1974b, Redmann 1972). Some of the species with which it most frequently occurs are the following: *Allenrolfea occidentalis* (Wats.) Kuntze, *Aster ericoides* L., *Atriplex argentea* Nutt., *A. patula* L., *Chenopodium rubrum* L., *C. glaucum* L. ssp. *salinum* (Standl.) Aellen, *Glaux maritima* L., *Hordeum jubatum* L., *Iva annua* Michx., *I. axillaris* Pursh, *Juncus balticus* Willd., *Poa arida* Vasey, *Polygonum ramosissimum* Michx., *Puccinellia nuttalliana* (Schult.) Hitchc., *Ranunculus cymbalaria* Pursh, *Rumex crispus* L., *R. maritimus* L., *Salicornia rubra* A. Nels., *Sarcobatus vermiculatus* (Hook.) Torr., *Scirpus americanus* Pers., *S. paludosus* A. Nels., *Sonchus arvensis* L., *Spartina gracilis* Trin., *S. pectinata* Bosc., *Sporobolus airoides* Torr., *Suaeda calceoliformis* (Hook.) Moq., *Triglochin maritima* L. (Flowers 1934, Tolstead 1942, Rawson and Moore 1944, Keith 1958, Bolen 1964, Dodd and Coupland 1966b, Hadley and Buccos 1967, Ungar 1965, 1967, 1970, 1974a, Ungar et al. 1969, Redmann

1972). Of these, the species with which *Distichlis stricta* is most consistently associated are *Hordeum jubatum*, *Puccinellia nuttalliana*, and *Suaeda calceoliformis*.

2.2.2 Species zonation with respect to soil conditions

Most inland salt flats or marshes have conspicuous zones of vegetation surrounding them. The distribution of species in these zones appears to be controlled by their tolerance to soil moisture and salinity (Ungar 1970, 1974a). The most saline soils are generally located in the center of the salt flat, and are typically barren (Schaffner 1898, Coupland 1950, Redmann 1972). Primary invaders of the barren flats are *Suaeda calceoliformis*, *Salicornia rubra* and *Sesuvium verrucosum* Raf. (Dodd and Coupland 1966b, Ungar 1966, 1967, 1968, 1970, 1974a, Hadley and Buccos 1967, Ungar et al. 1969, Redmann 1972). A zone of dwarf *Distichlis stricta* is commonly found next to the invading species (Ungar 1967, 1970, Ungar et al. 1969), and may be accompanied by *Polygonum ramosissimum* (Ungar 1967) or *Puccinellia nuttalliana* (Ungar 1970). *Triglochin maritima* with *Ranunculus cymbalaria* or *Puccinellia nuttalliana* may replace the dwarf *Distichlis stricta* zone (Dodd and Coupland 1966b, Ungar 1974a). In areas of lower salinity, tall *Distichlis stricta* may be found accompanied by *Hordeum jubatum*, *Atriplex patula*, *Iva annua* and *Poa arida* (Dodd and Coupland 1966b, Ungar 1966, 1967, 1968, 1970, 1974a, Hadley and Buccos 1967, Ungar et al. 1969, Redmann 1972). On well drained sites with even lower salinity, a zone of *Sporobolus airoides* or *Agropyron* species is usually found (Dodd and Coupland 1966b, Ungar 1966, 1968). This zone blends into typical prairie communities (Ungar 1967, 1968). Where standing water is present, *Scirpus paludosus* is usually found in the most saline areas, and *Spartina pectinata*, *Phragmites communis* Trin., *Juncus balticus*, *Eleocharis palustris* (L.) R. & S., and *Carex* species occupy less saline sites (Bolen 1964, Dodd and Coupland 1966b, Ungar 1967, 1968, 1970). Saltgrass can survive in a wide range of soil conditions, but it is most prevalent where soil moisture and salinity are high. The soils under *D. stricta* are usually well supplied with moisture because of high water tables, which are often from 30 cm to 1 m below the soil surface (Kearney et al. 1914, Aldous and Shantz 1924, Shantz and Piemeisel 1924, Flowers 1934, Tolstead 1942, Billings 1945, Ungar 1965, Hunt and Durrell 1966, Redmann 1972). Although soil moisture is plentiful, soil salt concentrations are very high where saltgrass forms extensive, almost monospecific stands of dwarf plants (Aldous and Shantz 1924, Shantz and Piemeisel 1924, Flowers 1934, Tolstead 1942, Billings 1945, Nielsen 1953, Bolen 1964, Dodd and Coupland 1966b, Hadley and Buccos 1967, Redmann 1972, Ungar 1974a).

2.2.3 Vegetational analysis

Distichlis stricta communities on highly saline soils tend to be comprised of few species other than the dominant ones (Flowers 1934, Redmann 1972), while those on less saline soils are found with a greater variety of species (Ungar 1974b). Frequency values of saltgrass in both types of communities are usually 100% (Ungar 1965, 1967b, 1968, 1970, 1974a, Ungar et al. 1969). Frequency values of other species may range from 0 in dwarf saltgrass communities to 90% in communities in which saltgrass is a codominant (Keith 1958, Ungar 1965, 1968, 1970, 1974a, Dodd and Coupland 1966b, Hadley and Buccos 1967). Species in dwarf saltgrass communities usually have low cover values (Redmann 1972), while relative cover in tall saltgrass communities is generally much greater (Ungar 1965). Percent cover of *Distichlis stricta* typically ranges from 0.8 to 2% for the dwarf form, and from 7 to 11% for the tall form (Ungar 1965, 1967). Relative percent cover (i.e. proportion of total plant cover) of saltgrass may range from 84 to 100% in dwarf saltgrass communities and from 72 to 93% in tall saltgrass communities (Dodd and Coupland 1966b, Ungar 1968, 1970, 1974a, Ungar et al. 1969).

2.3 Halophyte Phenology

The edaphic factors which control halophyte distribution also strongly influence the life cycles of these plants. Soil conditions such as total salt content and moisture levels show definite seasonal trends (for example, see Ungar 1968) to which the plants must adjust if they are to successfully reproduce. The low number of families and genera represented in the halophytic flora (Waisel 1972) indicates that relatively few life strategies are capable of survival in areas dominated by high salt concentrations. The proportion of perennial species in halophyte communities is usually greater than the proportion of annual species, probably because perennials are more able to survive the fluctuations in soil conditions to which saline areas are subjected (Ranwell 1972).

Germination of halophytes is affected by salt concentration, temperature, and the type of salts present in the soil (Ungar 1978). Although halophytes are generally more tolerant than nonhalophytes at the germination stage, increases in salt concentration can delay germination and decrease the number of seeds germinating (Waisel 1972, Ungar 1978). Since most halophyte seeds can remain dormant until conditions are favorable, peaks of germination may occur when soil salinities are at their lowest levels, usually in early spring (Waisel 1972, Ungar 1978).

The date of initial growth of perennial halophyte species is influenced by temperature and soil conditions, and consequently varies somewhat from year to year. In North American inland halophyte communities, shoots usually appear from April to late May, and grow rapidly until soil moisture levels decrease and salt concentrations increase (Bolen 1964, Ungar 1965). Vegetative growth often takes precedence over sexual reproduction; plants spread rapidly during the growing season, usually by means of rhizomes or runners

(Ranwell 1972, Waisel 1972). In this manner halophyte clones, such as those of *Distichlis stricta*, can rapidly colonize unvegetated saline areas (Hansen et al. 1976). Rhizomes of *Distichlis stricta* produce fairly extensive root systems which may penetrate the soil to depths of three meters, where soil salinity is often lower (Robertson 1955).

Few studies have been done on timing and control of flowering of halophytes. Flowering appears to depend on many of the same factors which control flowering of nonhalophytes: light intensity, photoperiod, and temperature (Waisel 1972). Soil conditions may influence the timing and degree of flowering, but the extent of this influence is not fully understood.

2.4 Growth of Plants in Solution Culture With Added Salts

2.4.1 Use of solution culture

Plant growth can be carefully controlled and manipulated through the use of nutrient solutions. The advantages of soil-free growth systems are many (Epstein 1972, Gauch 1972). The use of solution cultures permits the study of ion uptake and chemical effects of the nutrient medium without the influence of soil or substrate physical effects. This can be especially useful in the study of salinity effects, since it can be used to determine the importance of salt concentration vs. soil structure in the growth of halophytes or glycophytes. Solution culture also allows precise control of the root medium, since nutrient concentrations and ratios can be attained and maintained with relative ease. Close control of pH and solution osmotic potential is also possible.

There are some drawbacks to growing plants in a soil-free system. The absence of soil biota may significantly affect growth of some species, and when roots normally have symbiotic associations with soil organisms, plant growth in solution culture may be difficult or impossible. Rooting patterns in liquid media may be quite different than those found in solid substrates, since water supply is not limiting. Also, it is not always possible to extrapolate from solution culture growth studies to plant behavior in the field. Nonetheless, soil-free growth studies aid in elucidating many of the factors important in plant growth and development, and provide an excellent method for the study of salinity effects.

2.4.2 Importance of cations in plant growth

Plant growth is largely determined by the composition of nutrients present in the rooting medium. Optimum growth depends on both the concentration of essential nutrients in soil or nutrient solution, and on their interrelationships.

Calcium is regarded as a macronutrient, even though the amount required for normal plant growth is quite low (Christiansen and Foy 1979). This element is involved in several important processes, including maintenance of membrane selective permeability, maintenance of chromosome structure, enzyme activation, and formation of cell walls (Hewitt and Smith 1974, Christiansen and Foy 1979). There is a great deal of variation in the amount of calcium required by plants; the type of plant and the conditions in which it is growing determine the amount required to eliminate deficiency symptoms (Loneragan et al. 1968, Loneragan and Snowball 1969a). Reported calcium levels in plant dry matter range from 0.005 to 2 me/g (Wyn Jones and Lunt 1967).

The role of calcium in membrane permeability appears to be crucial to plants growing in saline conditions. Work by several authors has shown that at high salinities, increased calcium levels are necessary to prevent calcium deficiency symptoms, restore cell growth and development, and prevent accumulation of toxic levels of sodium and other ions (Howard and Adams 1965, Hyder and Greenway 1965, Elzam and Epstein 1969a, LaHaye and Epstein 1969, Lund 1970, Gerard and Hinojosa 1973, Marschner 1974).

The relatively large amounts of magnesium required by plants are used for stabilization of ribosomal particles for protein synthesis, activation of enzymes involved in phosphorylation processes, and formation of chlorophyll (Hewitt and Smith 1974, Kirkby and Mengel 1976). Magnesium in dry plant tissue is usually present in concentrations from 0.08 to 0.42 me/g. When magnesium is present in soil (eg. serpentine soils) or nutrient solutions in abnormally high concentrations, severe nutritional problems may result due to magnesium toxicity and/or depressed calcium uptake (Walker et al. 1955, Lund 1970). The adverse effects of high Mg/Ca ratios will be discussed later.

Potassium is needed by plants in larger quantities than any other cation; it is the only univalent cation considered indispensable for all living organisms (Evans and Sorger 1966). Depending on species or genera, usually from 0.25 to 0.75 me/g of plant dry matter is made up of potassium, but concentrations as high as 1.25 me/g have been reported (Evans and Sorger 1966, ap Griffith and Walters 1966, Andrew and Robins 1969, Walker and Peck 1975). Although the specific functions of potassium are not clearly understood, its main role is probably related to specific effects on enzyme proteins, with secondary roles involving osmotic processes and pH control (Evans and Sorger 1966, Hewitt and Smith 1974). In saline soils and nutrient solutions, potassium is more likely to be deficient than abundant.

Some halophytes have been shown to require sodium as a micronutrient (Brownell 1965, 1968), and small increments of sodium may be beneficial to growth of crop plants, but it is not regarded as being essential to most plants (Evans and Sorger 1966). ap Griffith and Walters (1966) reported a range of 0.008 to 0.045 me/g sodium in tissue of several grass genera, with marked differences found among the genera. They suggested that grasses with high sodium potentials would exhibit a wide range in sodium contents depending on the environment, while those with low sodium potentials would always have low sodium contents. Collander (1941) studied the growth in nutrient solutions of plants of several ecological types and taxonomic groups, and found that halophytes were among the species which absorbed the greatest amount of sodium, even when several alkali cations were equally available. He suggested that there may be a correlation between the strong absorption capacity, or inability to exclude sodium, and the halophytic character which enables these plants to survive on saline substrates.

There is some disagreement in the literature as to whether plants respond to ion concentrations or ion ratios in soil or nutrient solutions. Bernstein (1970, 1975) stated that the absolute concentration of ions in solution is the key to plant response; when sodium concentrations increase in soils, calcium and magnesium concentrations decrease, leading to deficiencies of these elements. However, there is a considerable amount of work which emphasizes the importance of ion ratios in ion uptake by plants (Arnold 1969, Khasawneh 1971).

Adverse Mg/Ca ratios in nutrient or soil solutions may result in magnesium toxicity or poor calcium uptake, which may lead to calcium deficiency. Joffe and Zimmerman (1944) found that plants grew poorly in Solonetzic soils with high Mg/Ca. A soil sodium content of above 10% of the exchangeable cations resulted in plant injury or death even when Mg/Ca was decreased. This suggests that when sodium concentration is high, Mg/Ca must be very low to avoid salt injury.

Walker et al. (1955) followed the growth of agricultural and endemic serpentine plant species in soils or solutions where Mg/Ca ranged from 0.5 to 29. They found that while the yields of crop plants decreased markedly when Mg/Ca was high, the yields of the native serpentine species were hardly affected over a large part of the range. They attributed this to the much greater absorption of calcium at low calcium levels by serpentine species compared with crop plants.

The importance of the Mg/Ca ratio in growth of sugarbeets was stressed by Mostafa and Ulrich (1976). They varied solution Mg/Ca from 3 to 0.4, and found that the high ratios resulted in calcium deficiency symptoms even when calcium concentrations exceeded amounts needed for normal growth. Magnesium interfered with calcium uptake and prevented adequate amounts of calcium from reaching plant tissues. Carter (1977) found that barley yields were reduced, and plants showed signs of Ca deficiency when Mg/Ca ratios were higher than 1 in nutrient solutions. There was strong correlation between Mg/Ca levels in tissue and those in solution.

The calcium to total cation (Ca/TC) ratio is closely related to the Mg/Ca ratio, since when solution Mg increases with respect to Ca, the level of Ca with respect to total cations decreases if other concentrations are held constant. Several authors have found that when Ca/TC reaches a critically low level, plant growth is reduced. Walker et al. (1955) found that little or no growth of crop plants occurred on serpentine soils and in nutrient solutions when calcium dropped below 10% of total cations, and between 10 and 20% yields were greatly depressed. Yields of serpentine species were not appreciably different within a Ca/TC range of 6 to 82%, and Ca/TC of 3 to 5% only moderately reduced their growth.

Howard and Adams (1965) found that the amount of calcium required for cotton root growth into subsurface media depended on the Ca/TC ratio rather than calcium concentration alone. A Ca/TC of between 0.10 and 0.15 was required in all cases. Working with barley in solution culture, Carter (1977) found that decreasing Ca/TC resulted in decreased growth regardless of the salinity level of the solution. Yield was well correlated with solution Ca/TC but not with solution calcium concentrations. When Ca/TC was low, calcium deficiency symptoms occurred even when the calcium concentration was relatively high.

There is little information available concerning the importance of soil cation ratios to growth of halophytes. Like serpentine plants, they may have more efficient nutrient absorption mechanisms than crop plants, enabling them to grow in a wider range of ion ratios.

2.4.3 Cation uptake from soil and culture solutions

Cations move from the soil solution and/or exchange complex to roots via the processes of mass flow, diffusion, and contact exchange (Epstein 1972), while only the first process is possible in nutrient solutions. Transpiration by plants may cause mass flow of soil solution or nutrient solution to plant roots. At high solute concentrations in soil solutions, soluble ions probably move directly into cell wall free space without being exchanged for on root colloid exchange sites. In nutrient solutions with high solute concentrations, cations move to the root surface by diffusion and transpiration pull.

The ion transport system of plants must provide desirable proportions of ions for nutrient requirements and osmotic adjustment to the rooting medium. Movement of ions from the solution-root interface into root cells depends on membrane permeability and selectivity, and electrochemical gradients (Waisel 1972). Most research on ion uptake has been done using excised roots or whole plants of common agricultural species. Epstein and Jefferies (1964) suggested that since these plants have been bred for high yield under conditions of ample nutrient supply, they may be less competent and versatile in absorbing nutrients than wild species which have been subjected to selective pressures of limited nutrient supplies. However, this research may demonstrate some basic principles of ion uptake mechanisms which may also operate in nonagricultural plants.

Numerous studies have demonstrated the existence of a dual mechanism of ion uptake by roots (Elzam and Epstein 1969b, Laties 1969, Elzam 1971, Rains 1972, Epstein 1976). At low solute concentrations (usually less than 0.5 mM) mechanism 1, which has a high ion affinity, is in operation. Ion uptake by this mechanism is shown by a smooth curve when concentration of the substrate is increased. At solute concentrations from 1 to 50 mM, the low affinity mechanism 2 comes into play. Increasing substrate concentrations result in stepwise increases in ion uptake by this mechanism.

Rates of calcium absorption must be maintained at constant levels to prevent calcium deficiency in growing plants, since once calcium enters shoots it is relatively immobile (Loneragan and Snowball 1969b). While some plant roots can actively absorb calcium (Maas 1969), those which cannot are more influenced by concentrations at the root surface due to diffusion and mass flow of nutrient solution (Marschner 1974, Kirkby 1979). Calcium uptake from solutions can be reduced by increasing concentrations of potassium or sodium (Johansen et al. 1968, Maas 1969, Elzam 1971).

Mass flow is probably more important than diffusion in moving magnesium ions in the soil solution to the root surface (Kirkby and Mengel 1976). Ferguson and Clarkson (1976) showed that in barley roots the patterns of uptake and translocation of Mg in different regions of the root were very similar to those of Ca. Translocation of both

Mg and Ca to the shoot was reduced once the epidermis had become suberized. Even though magnesium was more mobile than calcium, it did not move readily through the symplast of the root.

There appears to be some degree of competition between potassium and sodium for uptake, depending on their relative concentrations and the presence of other ions. Black (1956,1960) studied the effects of sodium chloride in solution culture on uptake of ions by two halophytes, *Atriplex hastata* and *A. vesicaria* . He found that at equimolar concentrations of Na and K, ion uptake by the former species resulted in leaf K content of three to four times the Na content. For the second species, more Na than K was absorbed at high equimolar Na and K concentrations, but when Na concentration was low, K could effectively compete with Na, and was accumulated at levels considered to be luxurious.

Working with *Avicennia marina* (mangrove), a marine halophyte, Rains and Epstein (1967a) found that the rate of K absorption from 0.02 to 1.5 mM was that which would be expected for mechanism 1. At higher K concentrations much higher rates were reached, indicating the operation of mechanism 2 which had a lower K affinity. Both mechanisms showed preferential affinity for K, which is needed in large amounts by this species; they were little affected by the presence of sodium.

Elzam and Epstein (1969b) found both mechanisms 1 and 2 operating in K absorption by roots of two species of wheatgrass. In both the salt tolerant species and the salt sensitive species, mechanism 1 showed a high K affinity and low Na affinity at low concentrations. In the salt tolerant species mechanism 2 absorbed both K and Na at a high rate, while in the salt sensitive species mechanism 2 absorbed K at a low rate.

At low to moderate levels of salinity, bidirectional pumps located at the plasmalemma may be able to raise K concentrations and lower Na concentrations inside cells (Pitman and Saddler 1967, Nassery and Baker 1972, Rains 1972). However, at high Na concentrations, Na uptake and content tend to increase at the expense of K uptake (Rains and Epstein 1967b, Elzam 1971, Storey and Wyn Jones 1978a, 1978b).

The role of calcium in ion transport cannot be overlooked. Many studies have shown that adequate Ca levels can increase uptake of beneficial cations such as K, while impairing entry to the cytoplasm of interfering cations such as Li, H and Na (Jacobsen et al.1960, Epstein 1961, Waisel 1962, Rains et al. 1964, Hooymans 1964, Carter 1977). The exact mechanism by which this is accomplished has not been elucidated, but it is believed that it involves alteration of the selective permeability of the plasmalemma by calcium (Waisel 1962). Although little work has been done on the effect of Ca on halophyte ion uptake, increased resistance of the plasmalemma to monovalent ions may be essential in these plants, since these ions may stimulate the loss of small molecules from plant cells by affecting carrier proteins or membrane permeability (Jennings 1976).

Concentrations of cations in shoot and root tissue of halophytes may reflect to some degree the concentrations and ratios in the external medium. Jefferies (1973) found that in *Triglochin maritima*, tissue concentrations of Na and Cl were related to external concentrations, but those of Ca and K were not. Hansen et al. (1976) found that Na and Cl tissue concentrations in *Distichlis stricta* more or less paralleled their soil concentrations in the early part of the growing season, and a nearly constant Na/K ratio was maintained. As plant vigor declined, Na and Cl tissue concentrations increased sharply while K concentrations decreased.

Various species of halophytes may accomplish ion uptake and salt tolerance by different means. These plants may regulate internal ion concentrations by excluding salts at the root surface (salt excluders), by extruding salts from specially developed salt glands (salt extruders), or by accumulating large amounts of ions for osmotic adjustment at high external ion concentrations (salt accumulators) (Greenway and Rogers 1963, Greenway 1968, Greenway and Osmond 1970, Greenway 1973, Albert 1975, Hansen et al. 1976, Flowers et al. 1977). It has been suggested that salt accumulators can grow more vigorously at high salt concentrations than excluders, since they can rapidly adjust to osmotic stress by increasing ion uptake (Greenway and Osmond 1970), while salt excluders or extruders must rely more heavily on organic solutes to lower their osmotic potentials (Flowers et al. 1977).

The reported research indicates that uptake of cations by halophytes depends on a variety of processes influenced by the concentrations and proportions of cations in the root medium. Mass flow and diffusion seem to be the primary means of ion movement to the root surface, where ions are absorbed selectively by high and low affinity ion uptake mechanisms. Membrane selectivity in many plants is enhanced by the presence of adequate proportions of calcium. Some salt tolerant species show high Na and K uptake at high salt concentrations, while others absorb K preferentially. Internal concentrations and ratios of cations may or may not reflect external ones, depending on the survival strategy of the species involved.

2.4.4 Osmotic and specific effects of added salts

Plants growing in saline solutions are affected both by the total salt concentration in the solution (osmotic effect) and by the type of salts and nutrient ratios present in the solution (specific effects) (Lagerwerff and Eagle 1961, Bernstein 1964, 1975, Lagerwerff 1969, Eaton et al. 1971). It is difficult to completely separate these effects, since low solution osmotic potentials caused by high salt concentrations are usually accompanied by unbalanced ion ratios. However, plants grown in isosmotic concentrations of single salts may react quite differently to different cation-anion combinations (Bernstein 1975). Magnesium salts depressed bean growth significantly more than sodium or calcium salts at isosmotic concentrations (Gauch and Wadleigh 1944). High calcium chloride concentrations were more injurious to bean plants than isosmotic concentrations of sodium chloride, while corn grew better in calcium chloride than in isosmotic solutions of Na, Mg or K chlorides (Bernstein 1964). Bean plants had higher yields when grown in isosmotic solutions of a non-permeating solute (Carbowax) than when grown in solutions of Na, Ca or Mg chlorides, probably due to the specific effects of the salts (Lagerwerff and Eagle 1961).

Since most halophyte species are widely distributed on soils of varying ion concentrations and ratios, it is likely that they are less affected by specific salt differences than are glycophytes. Their distribution seems to be controlled more by osmotic potentials of the soil solution (i.e. total cation concentration) than by the proportions of ions (i.e. cation ratios) contributing to the osmotic potential.

2.4.5 Water relations of plants grown with added salts

The low osmotic potentials of saline soil and culture solutions necessitate even lower values of total water potential in plant roots to allow for water uptake and turgor maintenance necessary for growth (Lagerwerff 1969, Bernstein 1975, Flowers 1975). Many studies have shown that cell sap osmotic potential of plants grown in saline solutions decreases as solution osmotic potential decreases. Eaton (1942) studied several crop plants in solution culture and found that decreases in tissue fluid osmotic potentials tended to parallel those caused in the solutions by additions of sodium chloride and sulfate. Ruf et al. (1963) found that when a non-permeating solute (Carbowax) was used in solutions, the cell sap of wheatgrass decreased about 90 kPa in osmotic potential for each 100 kPa decrease in the root medium. Janes (1966) found a similar pattern in bean and pepper plants grown in NaCl or PEG solutions, but when solution osmotic potential became too low, the plants could not decrease their sap osmotic potentials enough to maintain turgor. Using split-root cultures, Kirkham et al. (1969) showed that the degree of osmotic adjustment of bean and barley plants depended on the proportion of the root system exposed to saline conditions.

The manner in which plants respond to increased osmotic stress depends on the duration of the stress and on how quickly it is applied. Short term osmotic adjustment may involve rapid nonselective ion accumulation (Cooper and Dumbroff 1973, Storey and Wyn Jones 1978a) or increased potassium uptake (Bernstein 1963). Long term adjustment may depend on accumulation of large quantities of one or more cations (Berstein 1961, 1975, Cooper and Dumbroff 1973, Storey and Wyn Jones 1978a).

Many of these studies have been cited as evidence that plants can osmotically adjust to saline media, and that consequently turgor should be maintained and growth inhibition by salinity must be due to some factor other than water stress (Bernstein 1961, 1975). However, as Lagerwerff (1969) and Oertli (1966a, 1966b, 1968a, 1968b, 1976) have pointed out, cell sap osmotic potentials alone do not determine the water relations of plants in saline conditions, since water will enter the plant following a gradient of total water potential and not just osmotic potential. Oertli (1966b, 1968a) also suggested that expressed leaf sap is not necessarily a reliable indicator of vacuolar osmotic potential, since the sap is a mixture of both intra- and extracellular fluids. He believed that osmotic stress may indeed be an important cause of growth reduction due to salinity, since the continuous turgor adjustment needed by growing cells may be more difficult in saline conditions. Vacuoles must adjust in turgor not only to external solution osmotic potential, but also to solute accumulation in cell walls. This adjustment depends on salt transport, which may be rate limiting depending on solution composition.

Other studies indicate that plants growing in saline solutions may be subjected to water stress in spite of osmotic adjustment. Turgor pressure of crop plants often decreases as salinity levels increase (Hoffman and Jobes

1978, Cerda et al. 1979). Root permeability may also be greatly reduced by salinity, as O'Leary (1969) found with kidney beans in solutions with added NaCl. He also reported that salinity resulted in much greater leaf resistances to diffusion of water vapor than were found in plants grown in control solutions. Transpiration rates in several other species have been shown to be reduced by salinity due to high stomatal resistances (Gale et al. 1967, Ehlig et al. 1968, Kirkham et al. 1974). Plants growing under these conditions may be stunted due to decreased photosynthetic rates resulting from partial stomatal closure (O'Leary 1969).

Some halophytes adjust to salinity by massive ion uptake, while others rely on organic solutes to lower their osmotic potentials (Wallace and Kleinkopf 1974, Flowers 1975, Flowers et al. 1977, Storey and Wyn Jones 1978b, 1979). Osmotic potentials of halophytes in saline soils tend to be quite low, and often decrease as soil moisture decreases and soil salinity increases (Harris et al. 1924, Scholander et al. 1966, Dodd and Coupland 1966a, Wallace and Kleinkopf 1974). Increasing salinity levels may also reduce transpiration rates of halophytes. Webb (1966) found that at salinity levels above those needed for optimum growth, transpiration rates of *Salicornia bigelowii* when calculated on a fresh weight basis, were significantly reduced due to increased resistances to water movement. A salt requiring species of *Atriplex* was found to have lower root hydraulic conductivity, increased leaf resistance and reduced transpiration rates when grown in salinized culture solutions compared with unsalinized controls (Kaplan and Gale 1972). The authors suggested that the decreased transpiration rates enabled the plant to maintain high turgor pressures under conditions of high evaporative demand. This method of water conservation, which occurs in other halophytes, may be an effective adaptation to osmotic stress if the plants can maintain adequate photosynthetic levels.

2.5 Germination

Germination in saline conditons is influenced by several factors including total salt concentration in the germination media (osmotic effects), type of salt present (specific effects), and environmental parameters such as light and temperature (Ungar 1978). Although there may be consistent differences in salt tolerance between plant species and varieties at the time of germination, there appears to be no general relationship between the salt tolerance of seeds and tolerance during later phases of growth (Ayers and Hayward 1948, Abel and MacKenzie 1964, Rozema 1975a).

2.5.1 Osmotic effects

Numerous studies indicate that the decreasing osmotic potentials associated with increasing salinity result in both delays in germination and decreases in numbers of germinating seeds. Uhvits (1946) found that alfalfa germination was reduced by increasing concentrations of NaCl or mannitol, and that decreased germination corresponded to decreased water absorption by the seeds. Ungar (1962) studied seed germination in four succulent halophytes and found that while low concentrations of NaCl were stimulatory, there was a sudden drop in germination at higher concentrations. Increasing NaCl levels decreased germination of *Eurotia lanata* seeds from four stands in Utah, but some strains were more tolerant than others (Workman and West 1967). Both the rate and percentage of germination decreased for *Atriplex polycarpa* seeds when added NaCl resulted in osmotic potentials lower than -400 kPa (Chatterton and McKell 1969). Germination of seeds of *Iva annua* was inhibited by decreasing osmotic potentials due to decreased water uptake, but optimum germination also depended on optimum temperature (Ungar and Hogan 1970). Although *Puccinellia nuttalliana* seeds were able to germinate at an osmotic potential of -1600 kPa, there was a marked decrease in germination in four osmotica at an osmotic potential of -1200 kPa (Macke and Ungar 1971). Increasing salinity decreased germination of *Suaeda depressa* and *Hordeum jubatum* seeds and delayed germination up to several weeks depending on NaCl concentration (Williams and Ungar 1972, Ungar 1974c).

These studies show that while some added salts may slightly stimulate germination, they are not required, and optimal germination occurs when salinity stress is low even for very salt tolerant species. Maximum germination of halophyte seeds would occur in early spring when moisture levels are high and salt stress is low, favoring survival of some seedlings until the end of the growing season (Ungar 1977).

2.5.2 Specific effects

Several studies which compared different osmotica showed that some inhibit germination more than others. Choudhuri (1968) found that sodium carbonate was the most toxic and NaCl the least toxic, when their effects were compared with sodium sulfate and PEG on germination of some steppe plants. Younis and Hatata (1971) studied wheat germination, and found that when chloride and sulfate salts of Na, K and Mg were used, Mg salts were more inhibitory than K and Na salts at equivalent concentrations. Hyder and Yasmun (1972) found a similar order of inhibition of germination of alkali sacaton (*Sporobolus airoides*); inhibition increased from Na to Ca to K to Mg when Cl was the anion. Ryan et al. (1975) found that germination of four grasses was inhibited most by Mg and least by Ca salts, although the effects varied at different osmotic potentials.

2.5.3 Recovery of germination ability

When seeds have been placed in media with low osmotic potentials caused by specific salts, the recovery of their germination ability on removal from the media would indicate that the effect of the salts was osmotic rather than toxic. Hegarty (1978) suggests that failure of seeds to germinate at low osmotic potentials is the result of osmotic stress which may cause a form of induced dormancy. This dormancy can usually be overcome by removal of the stress or application of a stimulus (eg. treatment with a growth regulator such as gibberellic acid). Several papers provide evidence that many salts are not toxic to seeds of several halophyte species (Ungar 1962, Barbour 1970a, Ungar and Hogan 1970, Macke and Ungar 1971, Hyder and Yasmun 1972, Williams and Ungar 1972).

3. MATERIALS AND METHODS

3.1 The Physical Environment

3.1.1 Location of field study site

A site for the study of a *Distichlis stricta* community was chosen approximately 15 km east of Vegreville, Alberta, along the edge of Akasu (Sick Man) Lake (Figure 2). This location was selected for its abundance of saltgrass, relatively low level of disturbance, and accessibility. The field investigation, which included the growing season for saltgrass, was carried out from May to September, 1977 and 1978. In 1977 work was done on the descriptive aspects of the site including community characterization and phenology, while in 1978 quantitative micrometeorological and soils data were collected. All equipment was located in the midst of a zone of saltgrass on a peninsula which separated a shallow arm from the main body of the lake (Plate 1).

3.1.2 Meteorological data

From May to September 1978, temperature and humidity were continuously recorded by a hygrothermograph (Belfort Instrument Co.) placed at ground level in a white painted louvered shelter. Bihourly temperature measurements were used to produce a summary of daily and weekly maxima, means and minima. Weekly air temperature extremes at 10 cm and at the soil surface were measured with maximum-minimum thermometers (Taylor Instrument Co.). Precipitation

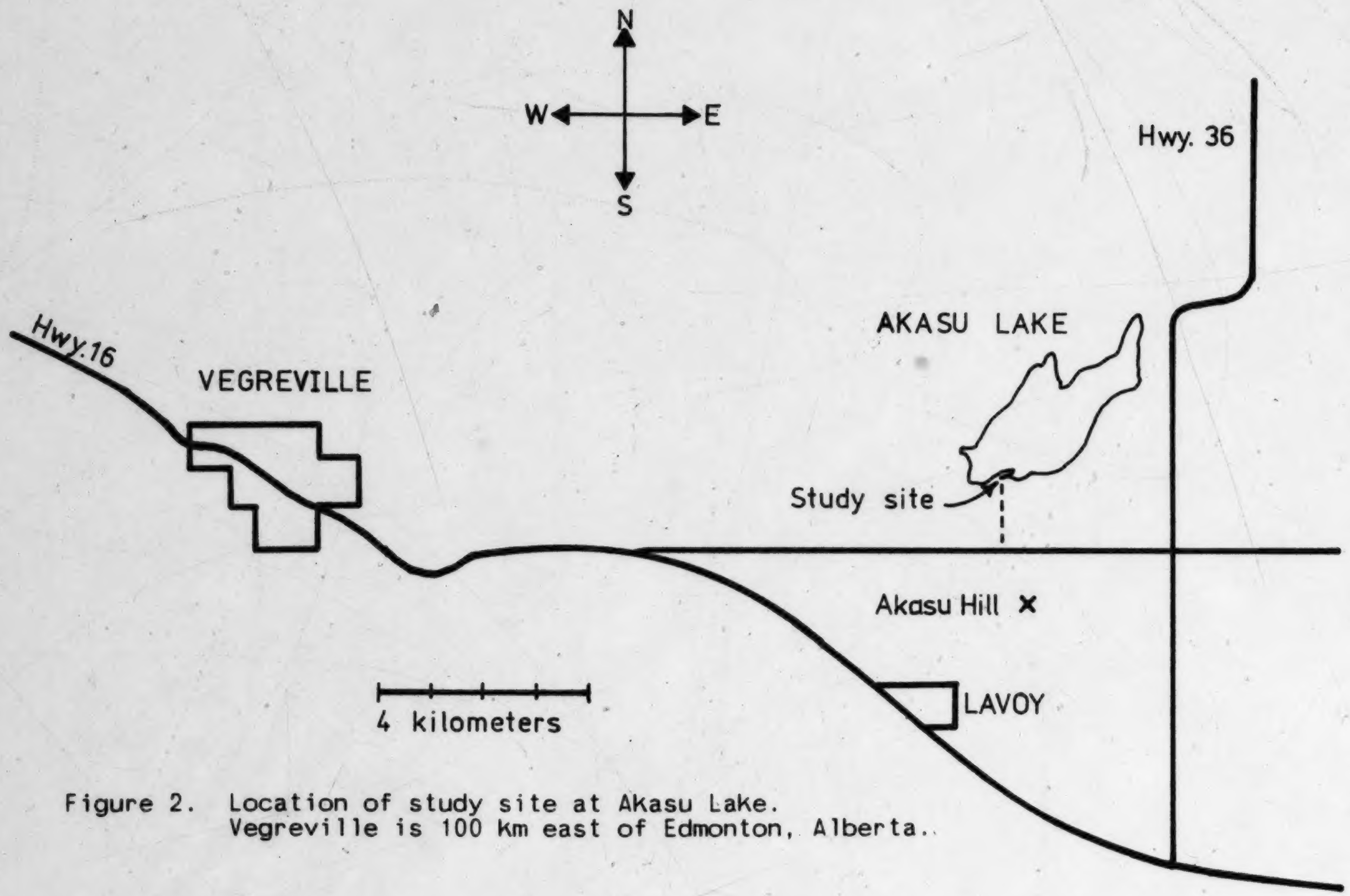

N
W
E
S
Hwy. 36
AKASU LAKE
Hwy.16
VEGREVILLE
Study site
Akasu Hill ×
LAVOY
4 kilometers

Figure 2. Location of study site at Akasu Lake.
Vegreville is 100 km east of Edmonton, Alberta.

Plate 1. Saltgrass field study site at Akasu Lake, Alberta.

measurements were obtained from the Canada Agriculture Soil Research Sub-Station located at Vegreville. Fluctuations in lake water level were recorded weekly at a water level stick placed about 6 m from shore.

3.1.3 Soil physical measurements

The large saltgrass zone was divided into three smaller zones based on growth form and density of saltgrass shoots (Figure 3). These small zones -- short *Distichlis stricta* (Ds), tall Ds and tall, scattered Ds -- were subject to detailed soil characterization.

Soil temperature in the three zones was measured for one week of each month with an eight probe Grant recorder (Grant Instruments Ltd.) which recorded hourly temperatures. The short and tall Ds zones each had three probes (at 2, 8 and 15 cm depths), while the tall, scattered Ds zone had two probes (at 2 and 8 cm).

One soil sample from the upper 10 cm of each zone was taken weekly for gravimetric moisture determination. The samples were sealed in preweighed soil tins, weighed, oven dried at 105 C for 24 to 48 hr, and reweighed to determine percentage moisture (Pw).

3.1.4 Soil chemical analyses

Every two weeks from May 26 to August 19, bulk soil samples were taken from the three zones of saltgrass. These samples were air dried, put through a soil grinder

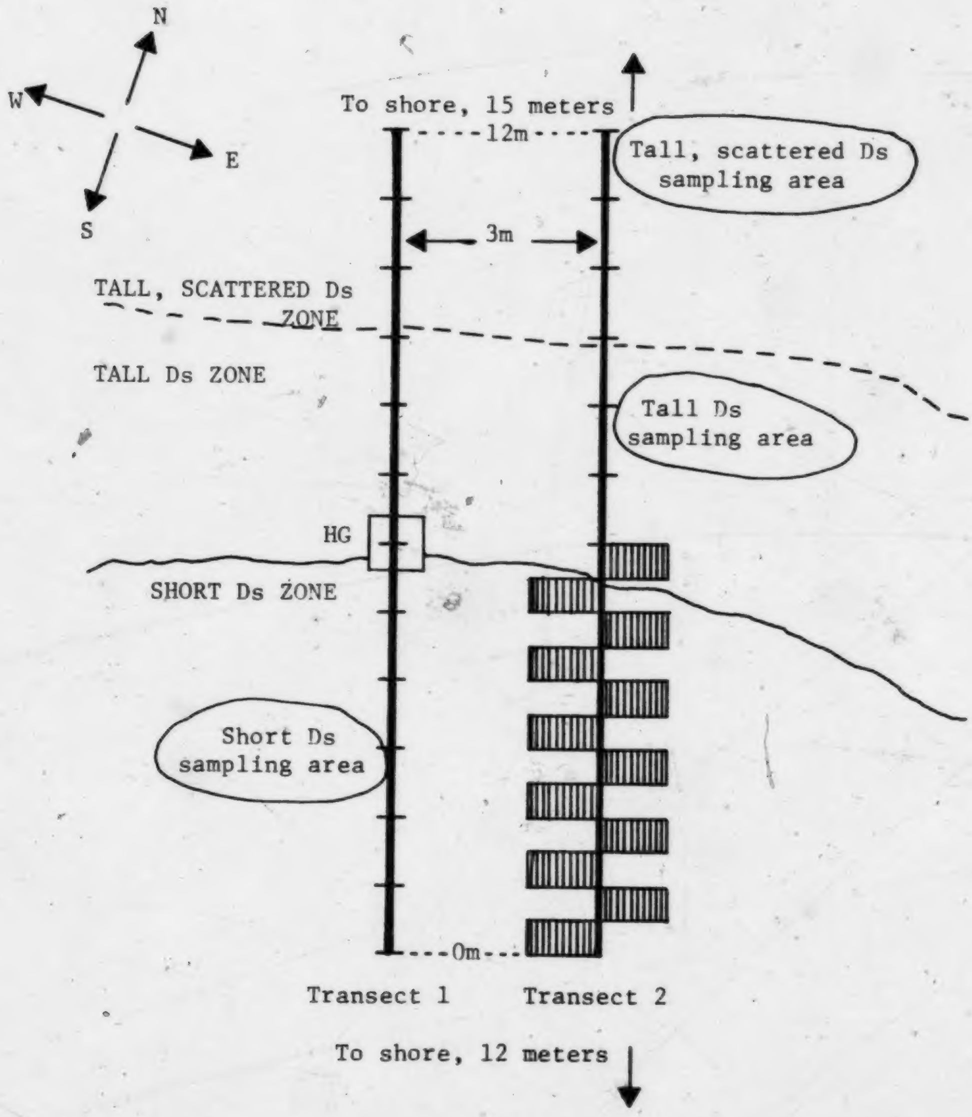

N
W
E
S
To shore, 15 meters
12m
Tall, scattered Ds sampling area
3m
TALL, SCATTERED Ds ZONE
TALL Ds ZONE
Tall Ds sampling area
HG
SHORT Ds ZONE
Short Ds sampling area
0m
Transect 1
Transect 2
To shore, 12 meters

Figure 3. Sampling areas and transects in saltgrass (Ds) community at Akasu Lake. Sampling detail is shown for the southern half of transect 2. Species percent cover was determined in the shaded areas. The three designated soil sampling areas are encircled.

(Robert B. Hewitt Welding & Repair) made into saturation pastes, and analyzed for pH, electrical conductivity, and cation concentration of the saturation extracts.

The saturation paste method was used rather than displacing or extracting the soil solution at field soil moisture levels, since saturation extracts can generally be removed much more quickly than the soil solution at field moisture levels. The use of saturation extracts in soil cation analysis has become quite standard, making comparisons among different soils possible. These comparisons are useful in establishing the degree of salt tolerance of native and agricultural species.

A saturation paste of each sample was made by adding distilled water to a weighed amount of air dry soil in a beaker (Richards 1954). The mixture was stirred with a metal spatula until all soil was moistened. At saturation the paste flowed slightly when the beaker was tipped, glistened at the surface, and when the spatula was inserted to make a trough the sides of the trough slid back together slowly. The beaker was then covered with a plastic bag and allowed to stand for one hour, after which the above characteristics were rechecked. The moisture content (saturation percent) of each saturated paste was determined gravimetrically. Soil pH was determined on the paste using a Beckman Zeromatic SS-3 pH meter (Beckman Instrument Co.). Initially these results were compared to those obtained from 1:2 soil:water mixtures. There was essentially no difference, therefore saturation pastes were used for pH readings, since it was necessary to prepare them for subsequent analyses.

Extracts of the saturation pastes were prepared using vacuum filtration (Richards 1954). Two layers of Whatman No. 1 filter paper were placed in a Buchner funnel and moistened with distilled water. Rinsed celite was added to decrease pore size. The saturation paste was placed in the funnel which was then covered securely with a plastic bag and vacuum filtration was applied until sufficient extract was collected. Depending on the soil type, this took anywhere from one to ten hours. Each extract was put in a glass vial with a drop of toluene and stored in a refrigerator until the analyses were carried out.

The electrical conductivity of the saturation extracts was measured with a YSI model 31 conductivity bridge (Yellow Springs Instrument Co.) A temperature correction factor, obtained by measuring the conductivity of a 0.01M KCl solution, was applied to give readings at 25 C.

Cation (Ca, Mg, Na, K) concentrations of the saturation extracts were determined with a Perkin Elmer model 503 atomic absorption spectrophotometer. An absorbance vs. concentration curve was prepared using known standards for each cation. Saturation extracts were diluted to appropriate concentrations, then absorbances were read and converted to concentrations in milliequivalents per liter (me/l) by using the appropriate dilution and concentration factors.

Initial soil anion analyses indicated that there was essentially no carbonate, only a trace of chloride, and very low levels of bicarbonate present in the soil saturation extracts. Almost all of the anion content consisted of sulfate ions. Since anion analyses involve procedures which can be inaccurate compared with cation determination by atomic absorption spectrophotometry, and since sulfate was consistently the major anion present, it was assumed that the sulfate content almost completely balanced the cation content in the soils being studied, and the analyses were not done.

Lake water samples were taken near the water level stick at two to three week intervals from June 2 to August 26. The pH of these samples was measured and cation concentrations were determined using the atomic absorption spectrophotometer as previously described.

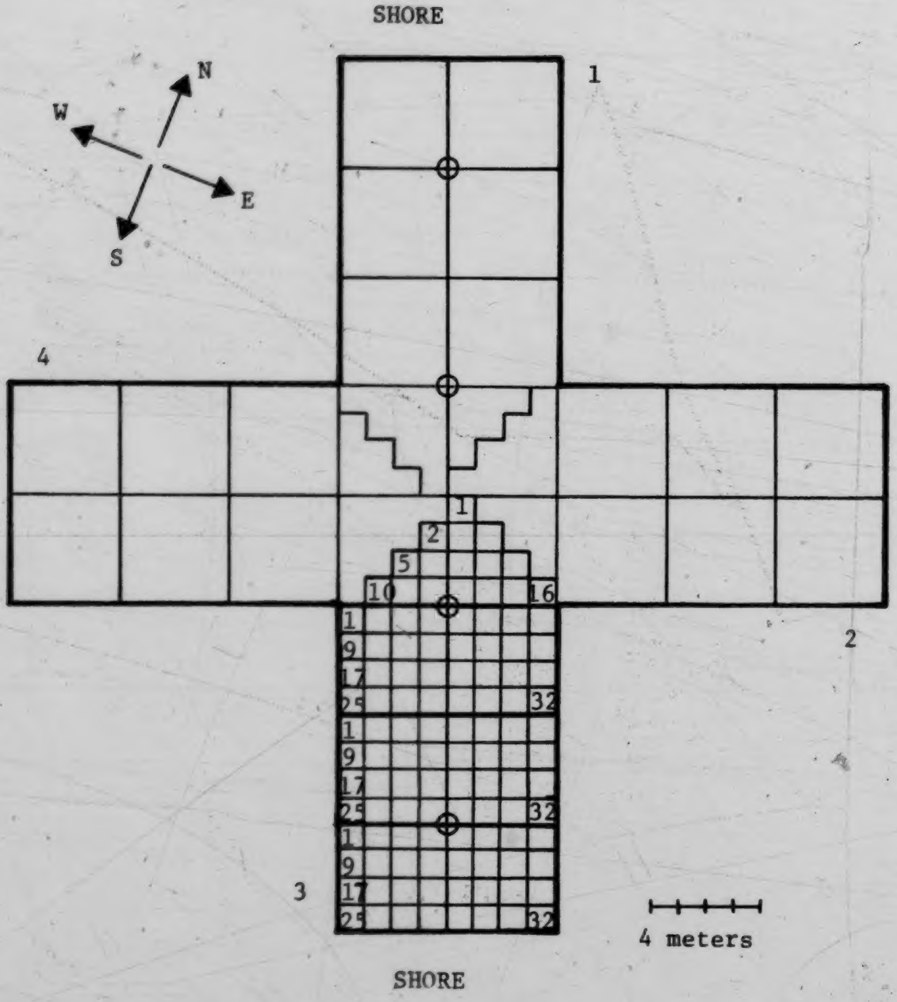
3.2 Community Characterization

3.2.1 Description of species present

In the summer of 1977, collections were made of the vascular plant species occurring in or near the *Distichlis stricta* community under study. The species were identified according to Moss (1959). A shore to shore transect on the peninsula through the saltgrass zone was described by listing species as they occurred in zones perpendicular to the transect line.

3.2.2 Community sampling system

A more quantitative community description than the foregoing was desired, so a 32 m by 32 m cross-shaped sampling area was set up in two areas on the peninsula. This system was designed to cover most of the distance from shore to shore across the peninsula, and to include samples from two strips which were perpendicular to each other. The center point of the first cross was placed near the hygrothermograph which was in the tall Ds zone, while the center of the second cross was in a short Ds zone farther east on the peninsula. The four 16 m arms radiated from the center point. The sampling area consisted of a 4 m wide strip on each side of the arms. Each arm was divided into four 4 m sections, each section having thirty-two 1 m by 1 m quadrats except for the sections closest to the center point which had sixteen 1 m quadrats (Figure 4). Quadrats were randomly chosen from the four sections, with a total of 12 quadrats per arm (4,4,3,1 from bottom to top of each arm). For the bottom half (i.e. 0.5 by 1 m) of each quadrat chosen, each species present was assigned to one of six cover classes (Oosting 1956). These classes were of the following magnitudes: 1) 1 to 5%, 2) 5 to 20%, 3) 20 to 40%, 4) 40 to 60%, 5) 60 to 80%, and 6) 80 to 100%. For each species recorded, frequency in each cross-shaped sampling area was determined. Soil samples of the top 15 cm were taken at each 4 m and 12 m point along the north-south arms of the transects.


SHORE
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1
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17
25
32
1
9
17
25
32
4 meters
SHORE

Figure 4. Detail of 32 m by 32 m cross-shaped sampling area. Each of four 16 m arms was divided into four 8 m wide sections, which were further divided into consecutively numbered 1 m quadrats. Percent cover was determined for randomly selected quadrats in each section. Soil samples were taken at circled points.

3.2.3 Saltgrass zone transects

In 1978, more intensive sampling was conducted in the main saltgrass community being studied. This was done using two parallel 12 m transects approximately 3 m apart (Figure 3). The center of each line was in the zone of tall Ds. Twenty-four quadrats of 0.5 by 1 m were sampled on alternate sides of each line as shown in Figure 4. For each quadrat, the percent cover of each species present was estimated to the nearest 5%, and frequencies were determined.

3.3 Growth of Distichlis stricta in the Field

3.3.1 Phenological observations

The phenology of *Distichlis stricta* was observed and described for the summers of 1977 and 1978. Observations were made of the approximate times of shoot initiation, flowering, and cessation of vegetative growth.

3.3.2 Shoot growth

As previously mentioned, the saltgrass community was divided into zones of tall and short saltgrass. These zones were rather arbitrarily separated on the basis of obvious differences in appearance of stands of saltgrass. There are no absolute height limits for short and tall forms because these forms are actually the endpoints of a gradient of culm height. The objective of this portion of the study was to compare the average heights of the two forms in this area.

Beginning in late May 1978, the growth of fifty shoots (culms) each of tall and short saltgrass was followed until there was no further increase in height and the shoots began to die back. Each shoot was tagged by taping a small numbered piece of cardboard around the base of the stem. Shoot height (measured to the tip of the longest leaves) was recorded each week for a period of seven weeks. The heights of shoots in the two groups were compared statistically by using a t-test program (ANOV10, Division of Educational Research Services, University of Alberta).

3.3.3 Flowering percentage

The percentage of flowering saltgrass plants was determined in both 1977 and 1978 for a short and a tall saltgrass zone. This was done by counting the total number of shoots and the number of male and female panicles in each of five 25 cm by 25 cm quadrats, and then converting the numbers to percentages. The flowering numbers and percentages were compared using the previously mentioned t-test program ANOV10.

3.4 Solution Culture Studies

3.4.1 Experiment 1

3.4.1.1 Experimental design

The first solution culture experiment was designed to test the effect of increasing the Mg/Ca ratio on the subsequent growth and tissue cation concentrations of *Distichlis stricta*. The composition of the four nutrient solutions is shown in Table 1. To obtain the desired concentrations of the major nutrients, six salts were used in varying proportions in the four solutions. These salts were potassium nitrate, calcium nitrate, ammonium phosphate, magnesium sulfate, sodium nitrate, and sodium sulfate. The electrical conductivity of the four solutions was measured using a conductivity bridge as previously described for soil extracts. The conductivity value (12.25 mS/cm at 25 C) was converted to osmotic potential using the calibration curve presented in Richards (1954). The osmotic potential of the four solutions was -486 kPa (-4.86 bars). The ionic strength (μ) of each solution was 0.296M.

All major nutrient concentrations, except magnesium and calcium, were held constant in the four treatment solutions. The sodium and potassium concentrations were chosen to represent the middle to lower end of the typical range of their concentrations in the field soil solution. The magnesium concentrations used were comparable to those at the low end of the field soil solution range, while the calcium concentrations in the treatment solutions included the entire range typically found in the field soil solution. The treatment solutions, like the soil solution,

Table 1. Composition of nutrient solutions used in Experiment 1. TC = total cation concentration. SAR = sodium adsorption ratio.

	Treatment Solution			
	1	2	3	4
Ions	Concentrations (me/1)			
Mg	40	60	70	75
Ca	40	20	10	5
Na	100	100	100	100
K	1	1	1	1
NH_4	4	4	4	4
TC	185	185	185	185
NO_3	41	41	41	41
H_3PO_4	4	4	4	4
SO_4	140	140	140	140
Ion ratios	Concentration ratios			
Mg/Ca	1	3	7	15
Ca/TC	0.22	0.11	0.05	0.03
Mg/TC	0.22	0.32	0.38	0.41
K/TC	0.01	0.01	0.01	0.01
Na/TC	0.54	0.54	0.54	0.54
SAR	15.8	15.8	15.8	15.8

The following micronutrient supplement was added to each solution.

Compound	ppm of element
H_3BO_3	0.5
$MnCl_2 \cdot 4H_2O$	0.5
$ZnSO_4 \cdot 7H_2O$	0.05
Na_2MoO_3	0.01
$CuSO_4 \cdot 5H_2O$	0.02

had sulfate as the dominant anion. A combination of ammonium and nitrate nitrogen was used. The ratio of nitrate to ammonium nitrogen was 10 to 1, which is within the range necessary for pH stability as suggested in Hewitt and Smith (1974).

The cation ratios used were chosen to greatly exceed the normal limits of growth of glycophytes. The range of Mg/Ca ratios extended from favorable (1) to much higher than was ever found in the soil solution at the Akasu Lake site (15). The corresponding calcium to total cation concentration (Ca/TC) ratios ranged from favorable (0.22) to the lowest found in the field soil solution (0.03). This low value is much lower than that generally regarded as adequate for plant growth (Carter 1977).

3.4.1.2 Preparation of plants

In late October 1977, dormant saltgrass plants with accompanying soil were collected from the short Ds zone at Akasu Lake. Clumps of soil with rhizomes and dead shoots were placed in pots, watered, covered with plastic bags, and stored in a dark cold room (-4 C) until ready for use. On April 14, 1978 the pots were placed in a lighted growth chamber (see below for description) and new shoots were allowed to sprout and grow until April 27. At this time rhizomes with shoots were carefully removed from the soil, rinsed with distilled water, and cut into segments.

Plastic 2 liter pots which had been made opaque with two layers of black plastic were filled with the appropriate treatment solutions. Two mls of FeEDTA solution (50 mg Fe per ml) and of the micronutrient supplement were added, and pH was adjusted to 6.0 with 1N NaOH. Seven 5 to 7 cm long shoots attached to short rhizome segments were placed in each pot. Each group of seven shoots was wrapped with foam rubber and inserted through a styrofoam cork in the plastic lid (see Figure 5). There were three replicates in each treatment. The twelve pots were placed in a growth chamber (Environmental Growth Chambers) with controlled temperature, humidity and light (Plate 2). Daytime (16 hr) temperature was 25 C and night (8 hr) temperature was 11 C. Relative humidity was maintained at 63%. Photosynthetically active radiation (PAR) as measured at shoot level with a PAR quantum sensor (Lambda Instrument Corp.) averaged 212 uE/m^2/s (46.2 W/m^2 -- for conversion see McCree, 1972) across the growth chamber.

All twelve pots in the growth chamber were connected to an air pump (Reciprotor) so that solutions were continuously aerated through Pasteur pipettes inserted through the pot lids. Distilled water was added as necessary to replace water lost through evaporation and transpiration. Growth data (shoot height, number of shoots and flowering shoots) were recorded weekly, and solutions were changed every two weeks.

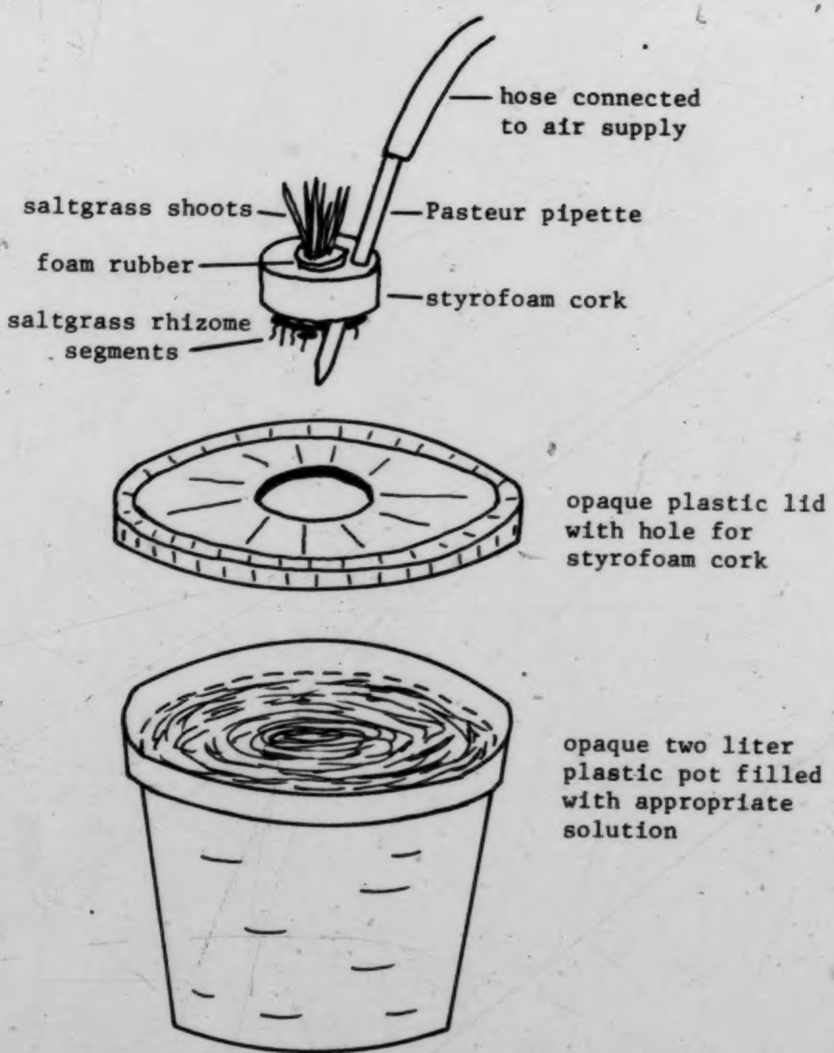
hose connected to air supply
saltgrass shoots
Pasteur pipette
foam rubber
styrofoam cork
saltgrass rhizome segments
opaque plastic lid with hole for styrofoam cork
opaque two liter plastic pot filled with appropriate solution

Figure 5. Placing of plants in container, solution culture Experiment 1.

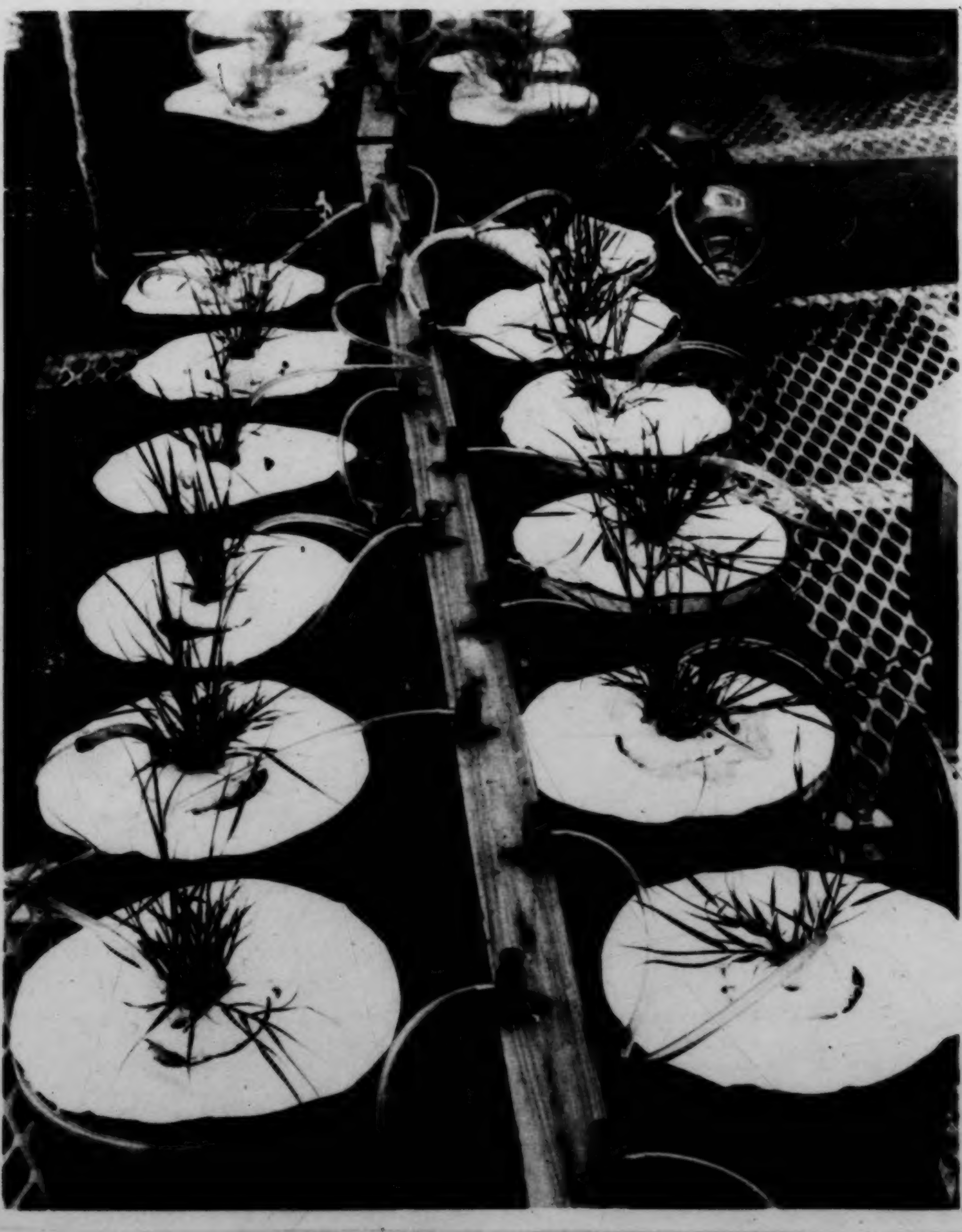

Plate 2: Pot set-up in growth chamber, Experiment 1.

3.4.1.3 Harvesting and tissue analyses

After six weeks of growth, the plants were harvested. For analytical purposes, the contents of each pot were treated as one plant. Plants were divided into two components: shoots, and rhizomes with roots. In order to simplify terms, the second component will be referred to as roots. Shoots and roots were rinsed separately in running distilled water for two to three minutes, placed in preweighed aluminum foil containers, and oven dried at 70 C for three days. Samples were then weighed to the nearest 0.001 gm to determine dry weights and ground with a tissue grinder (Arthur H. Thomas Co.). Tissue samples were dry ashed in a muffle furnace (Thermolyne Corporation) following the methods of Walsh (1971) and analyzed for cation concentrations as previously described for soil saturation extracts.

3.4.1.4 Statistical analyses

The statistical procedures followed were based on those described by Ferguson (1971). Dependent variables (growth variables, cation concentrations and ratios) from the four treatments were subjected to a one-way analysis of variance which included Scheffe multiple comparisons of observed means (ANOV15, Division of Educational Research Services, University of Alberta). In all cases a probability (p) value of 0.05 or less was required for the acceptance of a significant difference between means. Pearson product moment correlations between dry weight and cation variables were calculated using DEST01, obtained from the same source as ANOV15. Model 1 linear regressions (Sokal and Rohlf 1969) were calculated with BMD05R (Health Sciences Computing Facility, UCLA).

3.4.2 Experiment 2

3.4.2.1 Experimental design

The second solution culture experiment was designed to test the effects of three sodium concentrations and two levels of Mg/Ca ratio on growth and tissue cation concentrations of saltgrass. A basic nutrient solution (control) was also included to determine the effects of growing saltgrass with no added sodium. The composition of the seven nutrient solutions is shown in Table 2. The six salts listed for Experiment 1 and the iron and micronutrient supplements were again used in this experiment to obtain the desired nutrient concentrations. The osmotic potential of each solution was determined from conductivity readings as previously described.

The cation concentrations were mainly based upon typical field soil solution concentration ranges determined for the Akasu Lake site. The three sodium concentrations were chosen to cover the lower to upper ends of the field sodium concentration range. The potassium concentration used was higher than that in Experiment 1; it represents the upper end of the field range. The concentration of magnesium

Table 2. Composition of nutrient solutions used in Experiment 2. TC = total cation concentration. SAR = sodium adsorption ratio. μ = ionic strength, moles/liter. OP = osmotic potential, -kPa.

	Treatment Solution						
	A1	A2	A3	B1	B2	B3	C
Ions	Concentrations (me/l)						
Mg	30	30	30	30	30	30	2
Ca	6	6	6	30	30	30	8
Na	50	100	300	50	100	300	0
K	4	4	4	4	4	4	6
NH_4	4	4	4	4	4	4	2
TC	94	144	344	118	168	368	18
NO_3	34	34	34	34	34	34	14
H_2PO_4	4	4	4	4	4	4	2
SO_4	56	106	306	80	130	330	2
Ion ratios	Concentration ratios						
Mg/Ca	5	5	5	1	1	1	0.25
Ca/TC	0.06	0.04	0.02	0.25	0.18	0.08	0.44
Mg/TC	0.32	0.21	0.09	0.25	0.18	0.08	0.11
K/TC	0.04	0.03	0.01	0.03	0.02	0.01	0.33
Na/TC	0.53	0.69	0.87	0.42	0.60	0.82	0
SAR	11.79	23.57	70.71	9.13	18.26	54.77	0
μ	0.140	0.215	0.515	0.188	0.263	0.561	0.024
OP	270	400	970	320	440	970	60

was kept lower than that typically found in the field due to solubility limitations involved in preparing solutions with very high salt concentrations. The two calcium concentrations used represent the lower and upper ends of the field concentration range.

The Mg/Ca ratio of 5 used in part A represents one of the highest values found in soil saturation extracts during the growing season for saltgrass. It was felt that the decrease in Mg/Ca ratio from 5 to 1 in the treatment solutions would be large enough to influence growth and/or internal cation relations of saltgrass at increasing solution sodium concentrations.

The control solution was based on one developed by Johnson, et al. (1957). Although no sodium was added, sodium contamination from distilled water, air, and nutrient salts was unavoidable. No attempt was made to follow the exhaustive procedures designed to eliminate sodium outlined by Brownell (1965). Four nutrient salts -- potassium nitrate, magnesium sulfate, calcium nitrate and ammonium phosphate -- were used to prepare the control solution.

To determine whether or not the treatments with added sodium were detrimental or toxic to growth of a nonhalophyte, barley was grown in each treatment solution as a check. Barley was chosen because it is a common agricultural species, and although it is not a halophyte it can survive in moderately saline conditions (Carter 1977). Its death in the sodium treatments would indicate that these conditions could be toxic to many less tolerant species. Barley was also grown in the control solution to ascertain whether conditions in the growth chamber might be limiting.

3.4.2.2 Preparation of plants

Saltgrass plants in frozen soil were collected from the short Ds zone at Akasu Lake on February 28, 1979 (Plate 3). The frozen soil was soaked overnight in water. Rhizomes were removed from the soil, rinsed with distilled water, placed in large trays, and covered with vermiculite soaked with distilled water. The trays were placed in the growth chamber on March 1 under conditions previously described for Experiment 1, and new shoots were allowed to sprout and grow until March 14. At that time shoot height was approximately 4 to 7 cm.

On March 8, barley seeds were placed in vermiculite, soaked with distilled water, and allowed to germinate and grow. By March 14 the plants were at the one leaf stage, with shoot height of about 7 cm and root length of about 15 cm.

On March 14, plastic 2 liter containers which had been wrapped with two layers of black plastic were filled with the appropriate solutions and pH was adjusted to 5.5 with 1N NaOH. For each treatment solution, there were four pots (replicates) with saltgrass and one pot with barley. Saltgrass shoots were prepared as in Experiment 1. For each pot, ten shoots were wrapped with foam rubber and inserted

Plate 3: Collection of short D. stricta plants from frozen soil.

through a styrofoam cork. The "lids" for the pots were double layers of black plastic. In each pot, a layer of fiberglass screening was held by a rubber band so that it formed a support for rhizomes about 3 cm below the upper edge of the pot. The cork containing shoots with attached rhizome segments was inserted into the lid, and the lid was held to the pot with a rubber band (Figure 6). Pots of barley were prepared in the same manner, except that five shoots were placed in each pot, and no screening was necessary.

The 35 pots were placed in the growth chamber in the conditions described for Experiment 1. Growth progress was followed weekly and solutions were changed every two weeks until the end of the eight week experiment. As the rhizomes formed new shoots inside the containers, slits were made in the plastic lids to enable the new shoots to be brought into the light. Pots in which all plants died prior to the end of the experiment were removed from the growth chamber and their plants harvested as described in Experiment 1. Dead saltgrass plants were not separated into shoots and roots because they had little root development, and it was necessary to use the entire plants to provide samples of sufficient weight for dry ashing. Variables measured for dead plants were classified as shoot data.

3.4.2.3 Water potential measurements

The day before plants were harvested, water

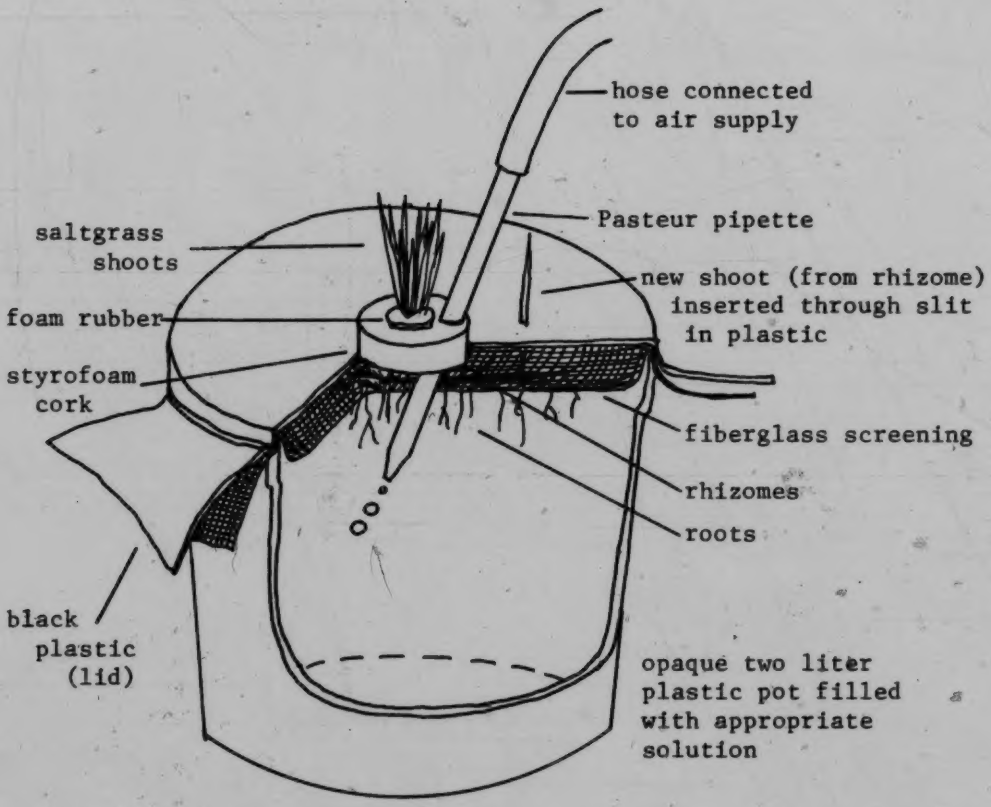
hose connected
to air supply
Pasteur pipette
saltgrass
shoots
new shoot (from rhizome)
inserted through slit
in plastic
foam rubber
styrofoam
cork
fiberglass screening
rhizomes
roots
black
plastic
(lid)
opaque two liter
plastic pot filled
with appropriate
solution

Figure 6. Cutaway view of container with plants, solution culture Experiment 2.

potential readings were taken for each surviving treatment using a pressure bomb (PMS Instrument Co.) following the techniques described by Scholander, et al. (1965). Readings were taken during the night portion of the daily cycle for ten shoots in each treatment solution. Immediately following the readings, shoots were rinsed with distilled water, blotted dry and placed in preweighed foil pouches for fresh weight determinations. They were then oven dried and added to the remaining shoot tissue for the replicate to which they belonged.

3.4.2.4 Harvesting and tissue analyses

At the end of the experiment, plants were harvested, dry ashed and analyzed as described for Experiment 1 (page 58), with the addition of blotting and then fresh weight determination immediately following the distilled water rinse. Water content of shoots was determined on an oven dry weight basis.

3.4.2.5 Statistical analyses

Dependent variables from the treatments were subjected to three statistical analyses. A two-way analysis of variance (ANOV25) including Scheffe's multiple comparisons of main effects was performed on data from treatments A1, A2, A3, B1, B2, and B3 where values from B3 dead plants were available. The lack of separate root data from treatment B3 precluded the use of the two-way ANOV on root data from the entire experiment, since there was an uneven number of root data groups. A one-way analysis of variance (ANOV15) which included Scheffe's multiple comparisons of group means was used to compare data from all the treatments including the control. Treatment B3 whole plant values were analyzed with shoot data since the plants, before they died, showed little or no root development. Occasionally it was necessary to substitute another one-way analysis of variance (ANOV11) where a variable included a group with zero variance, since ANOV15 dropped all such groups from the analysis. A correlation program (DEST01) was used to calculate Pearson product moment correlations between dry weight of shoots and roots and all cation variables. For all analyses, a probability (p) value of 0.05 or less was required for the acceptance of significance.

3.5 Germination

3.5.1 Experimental design

The germination experiment was designed to test the effects of decreasing water potentials and different types of osmotica on percentage germination of *Distichlis stricta* caryopses (seeds). There were four salts (sodium sulfate, magnesium sulfate, sodium chloride, polyethylene glycol) and five water potentials (0, -200, -500, -1000, -2000 kPa), with five replicates in each of the twenty groups.

The salts chosen included three that are found in areas where saltgrass grows. Sodium and magnesium sulfate are common in the Alberta soils where saltgrass is found, while sodium chloride is the more common salt of many saltgrass communities in the United States. The influence of a non-permeating osmoticum on germination was tested with polyethylene glycol (PEG 6000). The water potentials were chosen to provide a control (0 kPa), a low degree of osmotic stress (-200 kPa), degrees of osmotic stress which might be found in the field (-500 and -1000 kPa) and a high degree of stress (-2000 kPa) which would not frequently be experienced by saltgrass seeds in the field at the time of germination.

3.5.2 Preparation of solutions and seeds

Distilled water was used for all 0 kPa treatments. The concentrations of the salt solutions used to produce the decreasing osmotic potentials were determined by using osmosity values (Chemical Rubber Company Handbook of Chemistry and Physics, 1975-1976) to plot molarity of the salt in question versus molarity of NaCl. Since water potentials of sodium chloride solutions are known (Lang 1967), the molar concentrations of salt solutions at the required water potentials could be determined by interpolation. For PEG, a calibration curve from Thompson (1978) was used.

Preliminary trials indicated that scarification of saltgrass seeds was necessary for germination, and that the number of germinating seeds was greater in the light than in the dark. Consequently, for the experiment all seeds were scarified and given light.

Inflorescences of short Ds plants were collected at Akasu Lake on April 29, 1979. Each caryopsis was removed from its lemma and palea with forceps. Seeds were stored in glass vials at room temperature until used.

On June 4,1979 all seeds were disinfected by soaking in 0.5% sodium hypochlorite for about 10 minutes, then rinsed in distilled water for 15 minutes (Choudhuri 1968). Seeds were then allowed to dry and were scarified as uniformly as possible with fine grain disinfected sandpaper.

Twenty seeds were placed in each 9 cm petri dish on two layers of Whatman #1 filter paper, and 7 mls of the appropriate solution were added. There were 5 replicates for each of 20 treatments. Each dish was fastened with a rubber band, and to reduce evaporation loss, was placed in a small plastic bag also held on with a rubber band. The petri dishes were then placed in the growth chamber in the conditions described for solution culture Experiment 1. Dishes were checked periodically and germination (the visible emergence of the coleoptile and/or radicle) was recorded.

3.5.3 Recovery of germination ability

After two weeks in the various osmotica, all ungerminated seeds were removed from their dishes and placed in fresh dishes containing distilled water for eight days. This was done to determine the extent of recovery of germination ability by the seeds.

3.5.4 Statistical analyses

Both one-way and two-way analyses of variance were performed on the raw data (number of germinated seeds per dish). A two-way analysis of variance including Scheffe's multiple comparisons of main effects (ANOV25) was used to locate any significant differences between pairs of salts and pairs of water potentials. For each water potential, a one-way analysis of variance (ANOV15) was used to compare pairs of salts, while for each type of salt ANOV11 (which did not drop groups with zero variance) was used to compare pairs of water potentials. In all comparisons a p value of 0.05 or less was required for the acceptance of a significant difference between pairs of means.

4. RESULTS

4.1 The Physical Environment

4.1.1 Micrometeorological data

During the 1978 field season (May through August) daily maximum air temperatures ranged from 10 to 33 C, with a mean of 22 C, while daily minima ranged from 2 to 16 C, with a mean of 9 C. A weekly summary of air temperatures is presented in Figure 7. Daily minimum relative humidity varied from 38 to 100%, with a mean of 62% for the May through August period. The temperatures recorded by maximum-minimum thermometers (Table 3) indicate that temperature extremes at the soil surface were consistently two to six degrees Celsius warmer than above-ground temperature extremes. A total of 24.20 cm of precipitation fell during the 1978 field season at Vegreville, approximately 15 km west of Akasu Lake. This was distributed as follows: May 5.33 cm, June 4.51 cm, July 4.42 cm and August 9.94 cm. The water level of Akasu Lake dropped 20 cm from May 19 to August 26.

4.1.2 Soil physical measurements

Soil temperature measurements for June, July and August 1978 show that the zone of short saltgrass experienced the highest soil temperatures, followed closely by the tall saltgrass and tall, scattered saltgrass zones (Table 4). Soil temperatures at the 2 cm level fluctuated

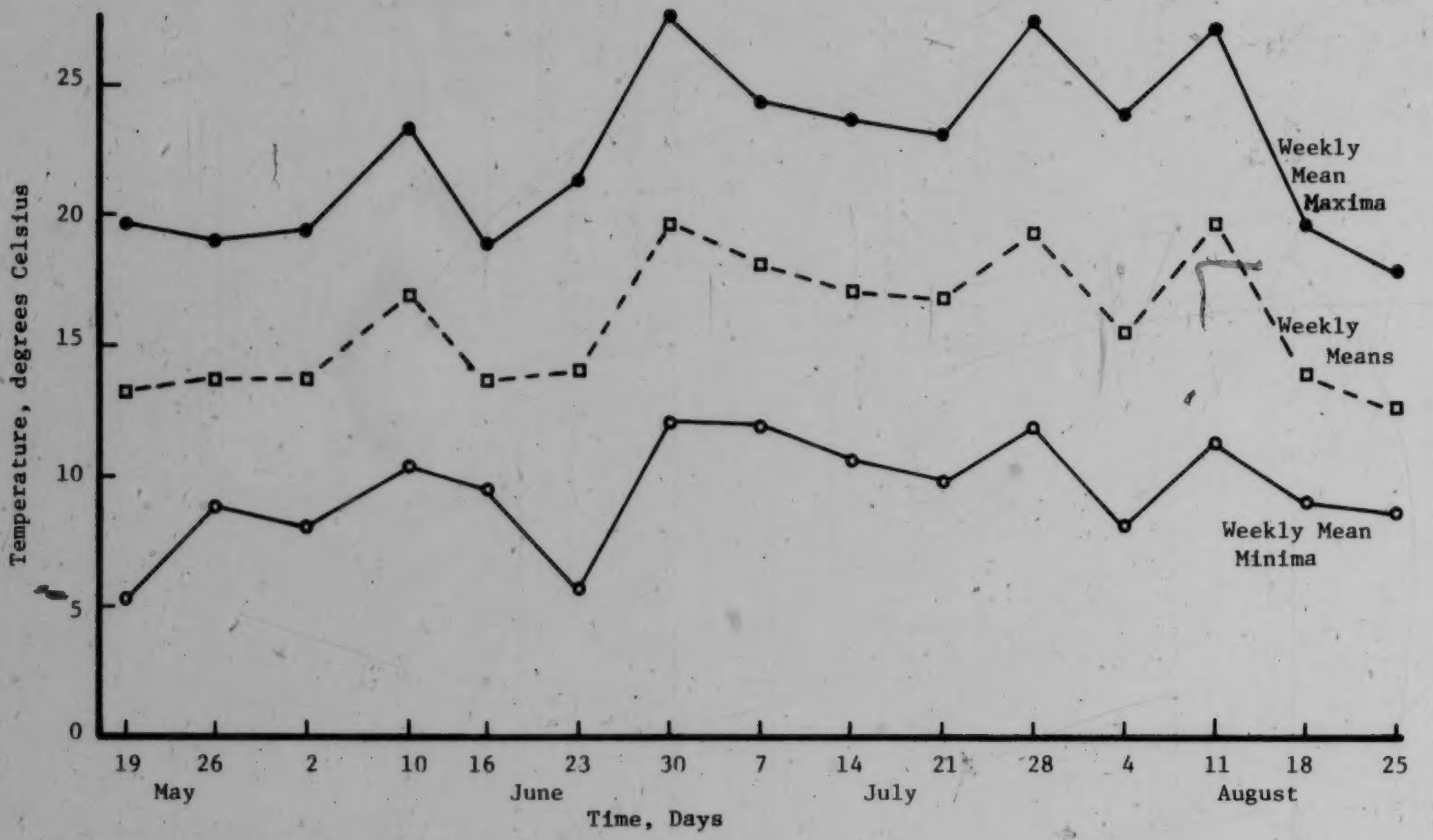

Figure 7. Summary of air temperatures at 10 cm at Akasu Lake site, summer 1978.

Table 3. Temperature extremes at Akasu Lake in summer, 1978. Readings were taken once a week from maximum-minimum thermometers placed 10 cm above ground (Air) and at the soil surface (SS). All temperatures are in degrees Celsius. The dates of the week during which the extreme occurred are listed below it in parentheses.

	Temperature Extremes			
	Maximum		Minimum	
Month	Air	SS	Air	SS
May	30 (20-26)	33 (20-26)	2 (13-19)	4 (13-19)
June	34 (24-30)	37 (24-30)	1 (17-23)	4 (4-10)
July	32 (22-28)	38 (22-28)	4 (8-14)	10 (8-14)
August	34 (5-11)	37 (5-11)	0 (29-4)	8 (29-4)
	Mean maximum		Mean minimum	
	Air	SS	Air	SS
May	28	31	3	6
June	29	31	5	8
July	30	36	6	12
August	29	32	4	9

Table 4. Soil temperatures of three saltgrass zones at Akasu Lake, 1978. Corresponding air temperatures (from hygrothermograph recordings) are also given. All temperatures are given in degrees Celsius.

Location and depth		Daily Maxima		Daily Minima		Daily Means	
		Range	Mean	Range	Mean	Range	Mean
				June 2-10			
Air (10cm)		17-31	25	8-13	10	14-22	18
Short Ds	2cm	18-26	23	11-16	13	15-21	18
	8cm	17-26	21	13-17	14	15-19	18
	15cm	17-23	21	12-16	14	14-19	17
Tall Ds	2cm	16-21	19	12-15	13	14-18	16
	8cm	15-19	17	12-15	13	14-16	15
	15cm	14-18	17	13-15	14	14-16	15
Scattered Ds	2cm	14-18	17	13-15	14	14-16	15
	8cm	13-17	16	11-13	12	12-14	13
				July 1-7			
Air (10cm)		18-30	24	9-15	12	13-22	18
Short Ds	2cm	18-28	25	16-18	17	17-22	21
	8cm	17-26	23	16-18	17	17-21	20
	15cm	18-23	22	17-19	18	17-21	20
Tall Ds	2cm	17-24	22	16-17	16	16-20	19
	8cm	17-22	21	16-18	17	16-19	18
	15cm	17-21	20	16-18	17	17-19	18
Scattered Ds	2cm	17-26	22	12-16	13	14-19	18
	8cm	15-21	19	13-16	14	14-17	17
				July 29-August 4			
Air (10cm)		15-30	24	5-14	8	11-18	16
Short Ds	2cm	18-25	23	11-16	13	16-19	18
	8cm	17-23	21	12-16	14	15-18	17
	15cm	17-21	19	13-17	16	16-18	17
Tall Ds	2cm	18-23	21	12-16	14	16-18	17
	8cm	17-20	19	13-16	14	15-18	17
	15cm	17-19	18	13-17	15	16-18	17
Scattered Ds	2cm	16-25	21	8-14	12	13-17	16
	8cm	15-19	18	11-14	13	13-16	15

more than those at the 8 and 15 cm levels, but considerably less than corresponding air temperatures. July soil temperatures were higher than those in June or August.

Soil moisture levels for all three saltgrass zones dropped to their lowest values from early July to early August (Figure 8). Soil in the tall Ds zone had the highest moisture percentages, while that in the tall, scattered Ds zone had the lowest. Soil from the short Ds zone consistently held less water at saturation than did soil from the other two zones (Figure 9). Comparison of field soil moisture percentages and saturation percentages showed that for the short and tall Ds soil zones, the amount of water in the field soils was about 66% of the amount held at saturation. For soil samples from the tall, scattered Ds zone, field soil moisture levels averaged about 33% of saturation levels.

4.1.3 Soil chemical analyses

The pH of samples from the three soil zones varied little during the field season (Figure 10). Soil from the tall, scattered Ds zone had an average pH of 8.00 from May 26 to August 19. The average pH for both the tall and short Ds zone soil samples was 8.35.

Analyses of saturation extracts from soil samples of the short and tall saltgrass zones revealed a consistent pattern in conductivity and cation levels during the field season (Figures 11 to 16). These levels were relatively high

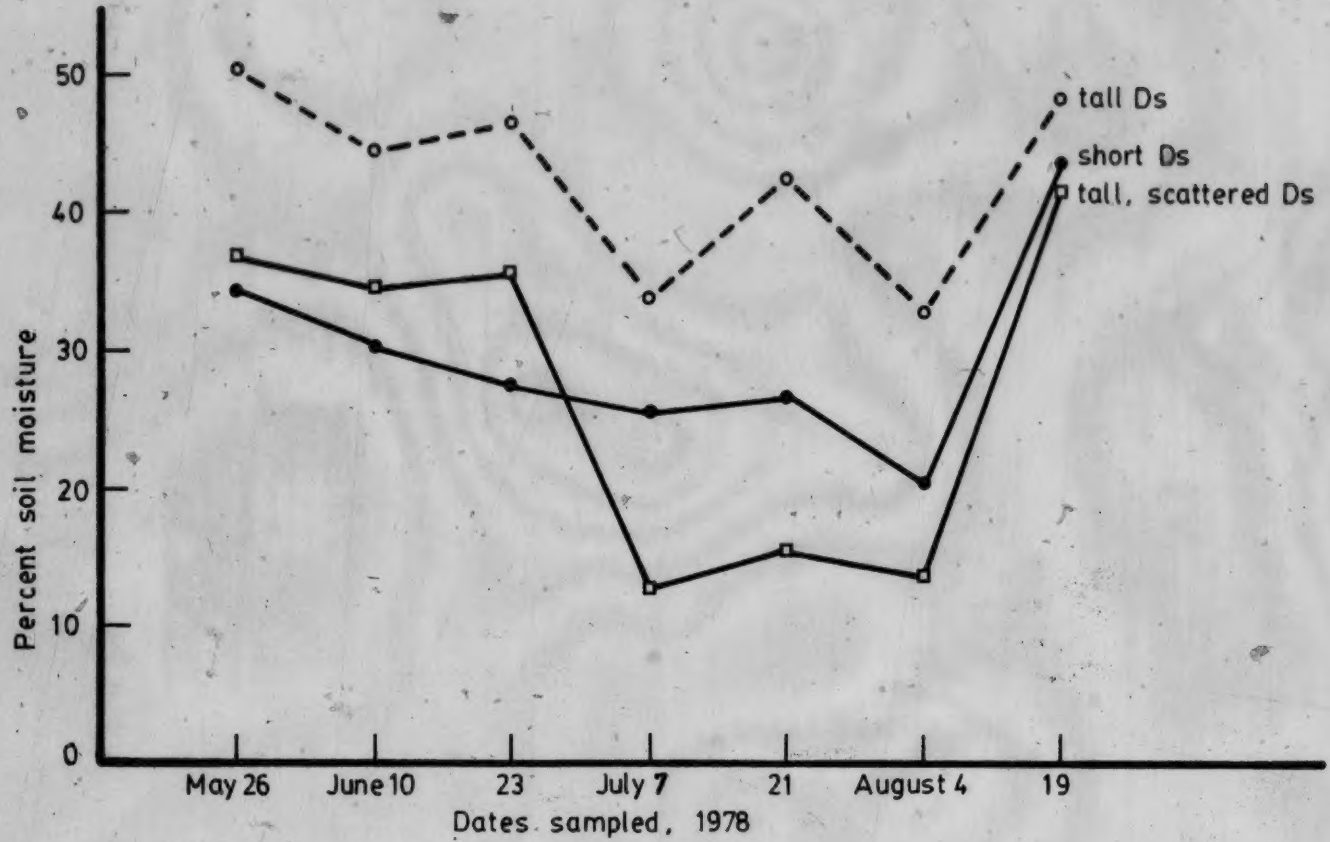

Figure 8. Percent soil moisture (Pw) of soil samples from three saltgrass (Ds) zones.

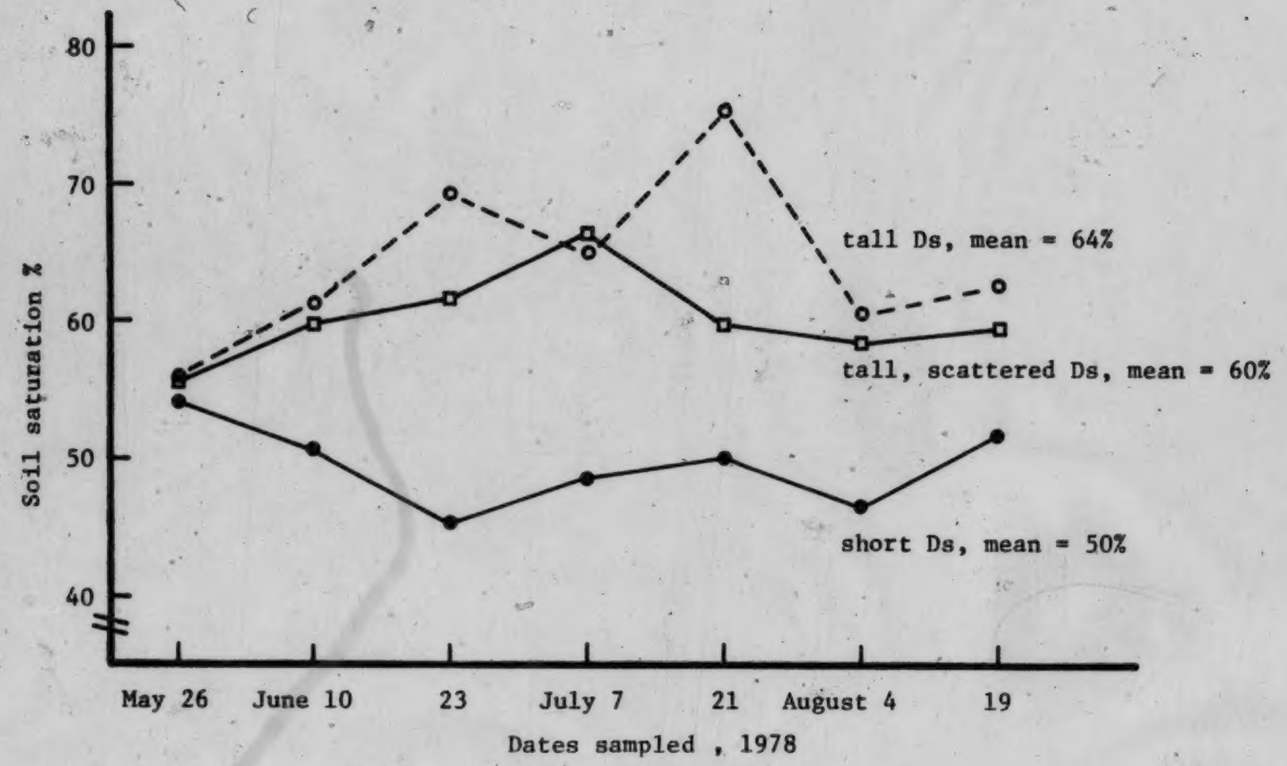

Figure 9. Saturation percentages of soil samples from three saltgrass (Ds) zones.

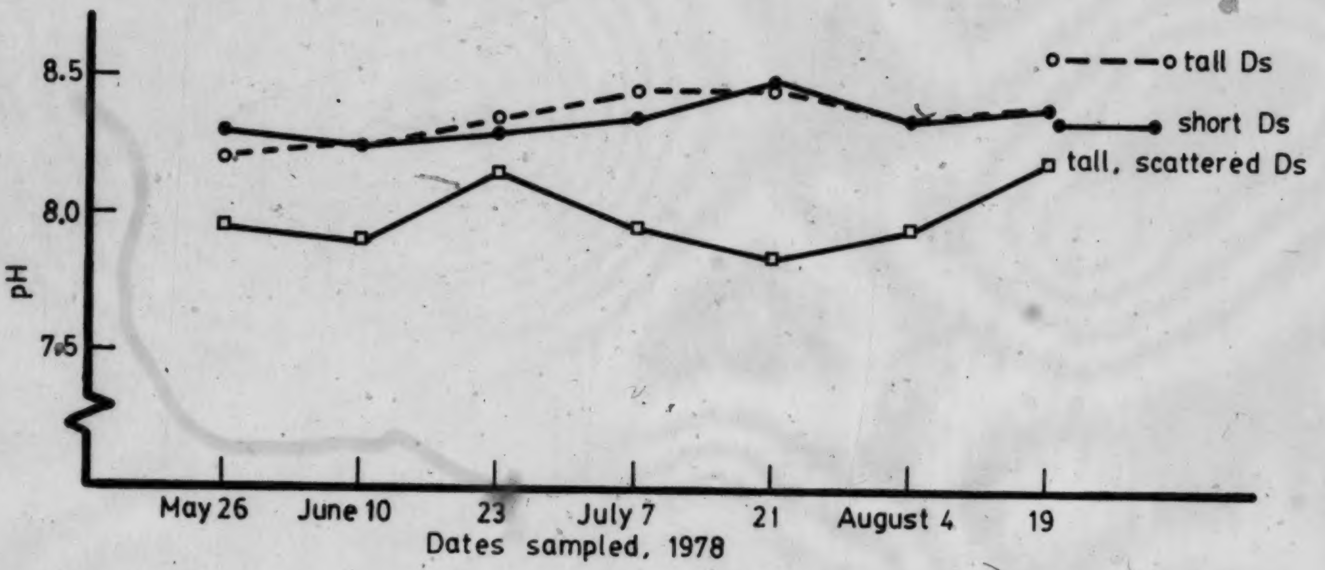

Figure 10. Saturation paste pH readings of soil samples from three saltgrass (Ds) zones.

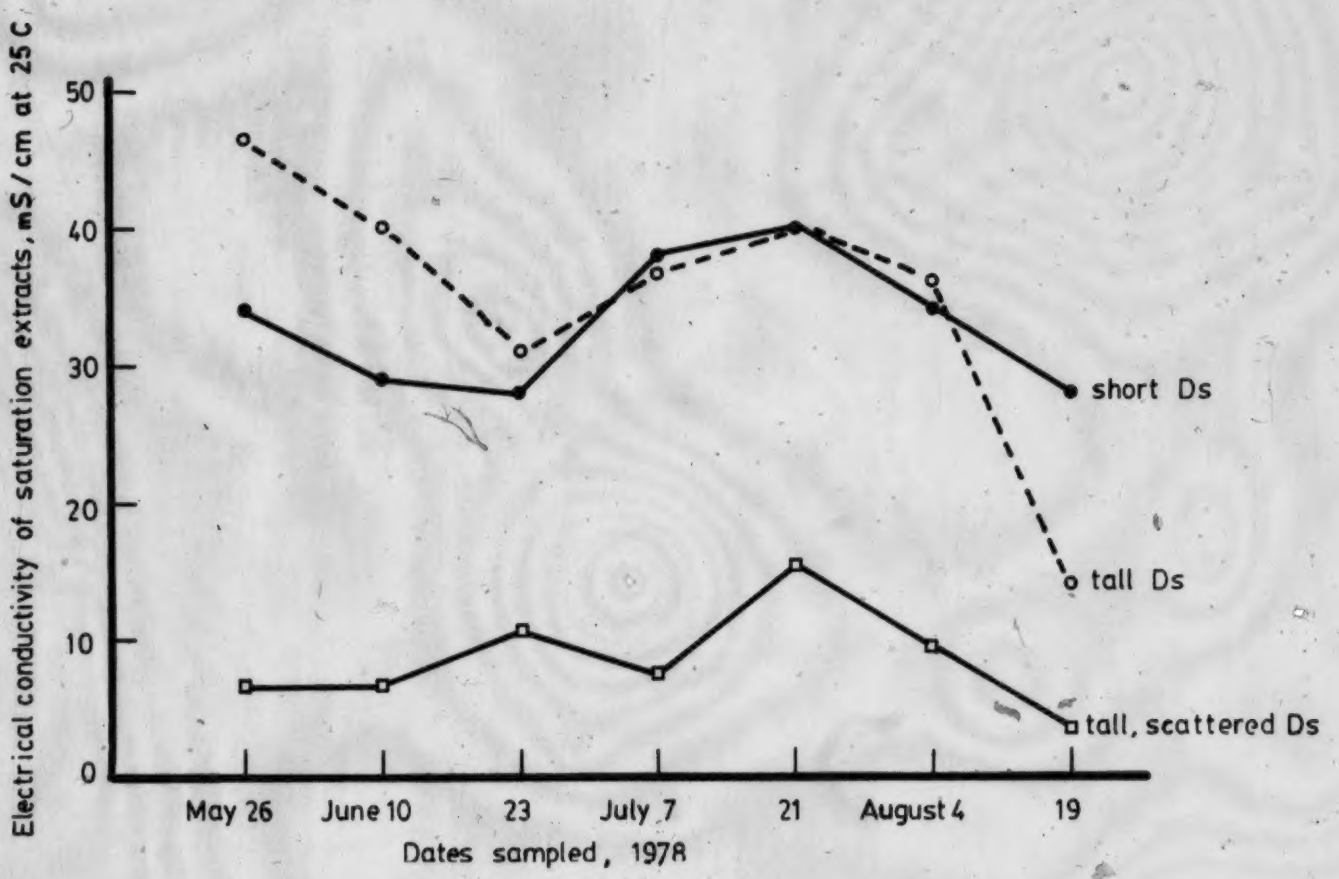

Figure 11. Electrical conductivity of saturation extracts (ECe) from soils of three saltgrass (Ds) zones.

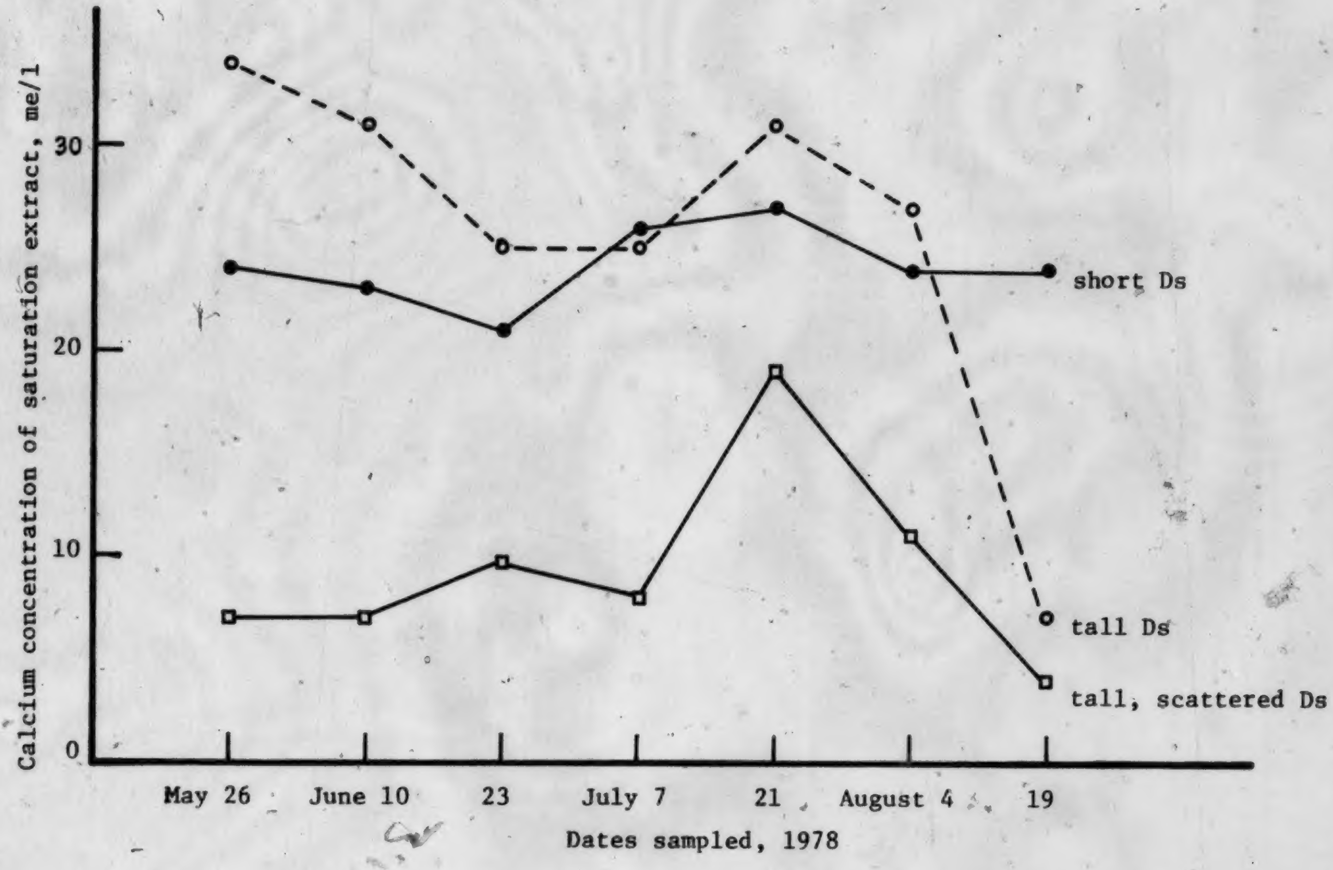

Figure 12. Calcium concentration of saturation extracts from soils of three saltgrass (Ds) zones.

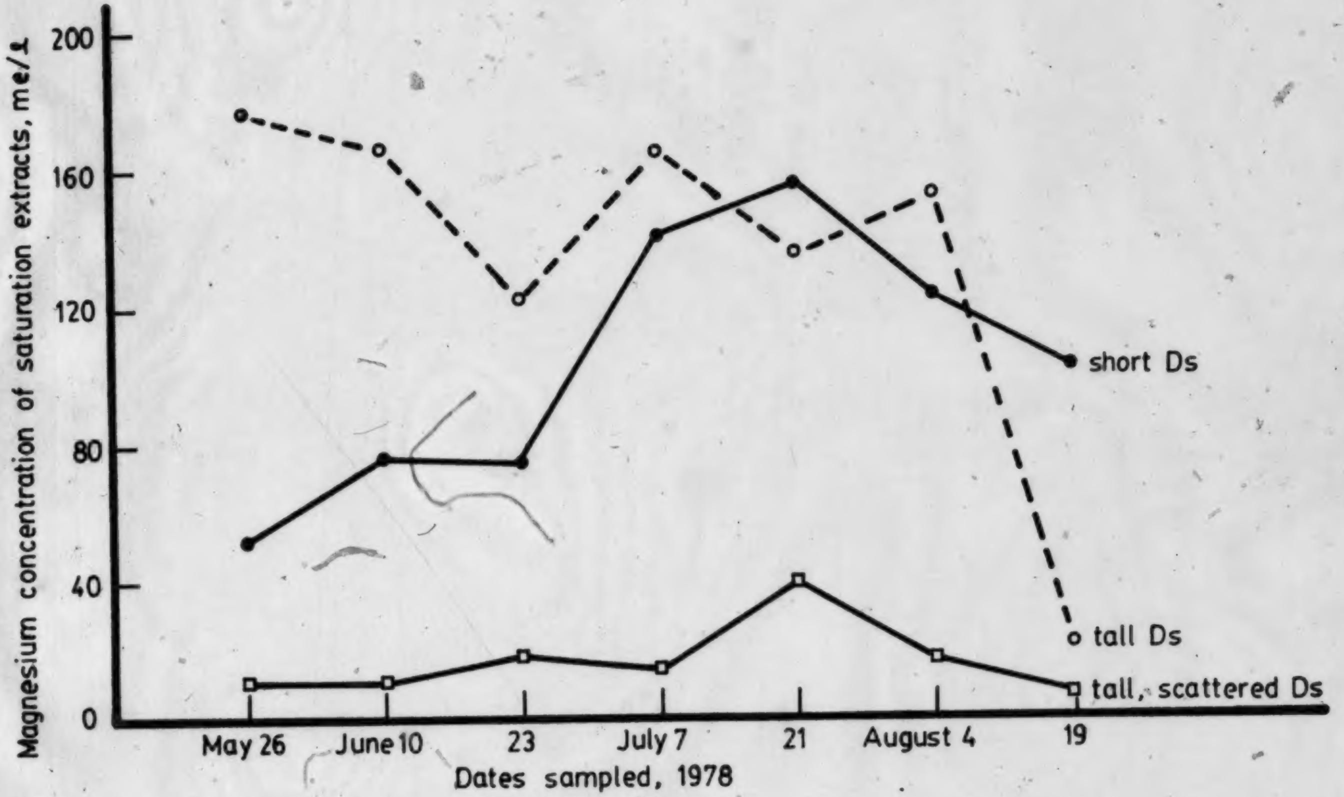

Figure 13. Magnesium concentration of saturation extracts from soils of three saltgrass (Ds) zones.

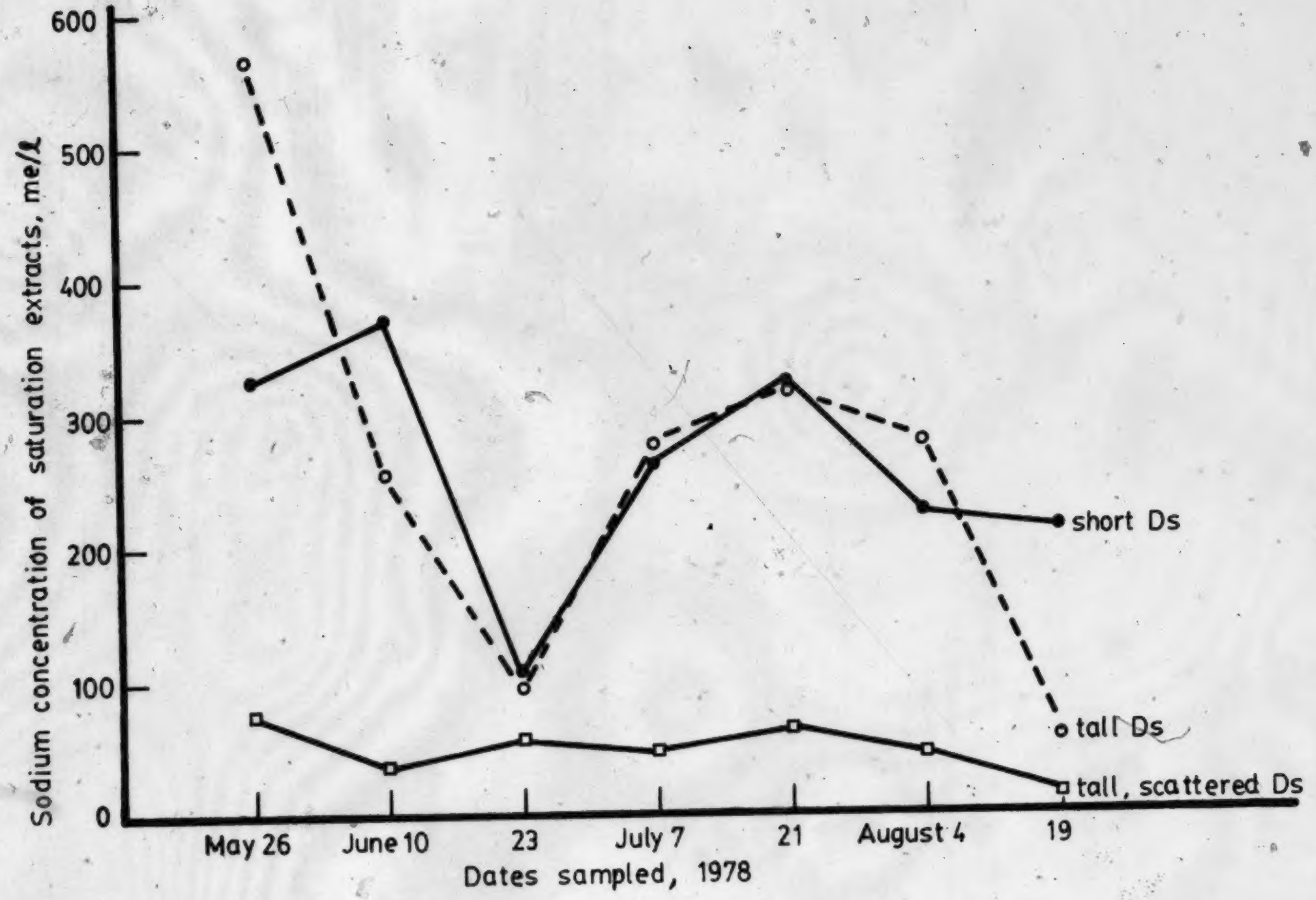

Figure 14. Sodium concentration of saturation extracts from soils of three saltgrass (Ds) zones.

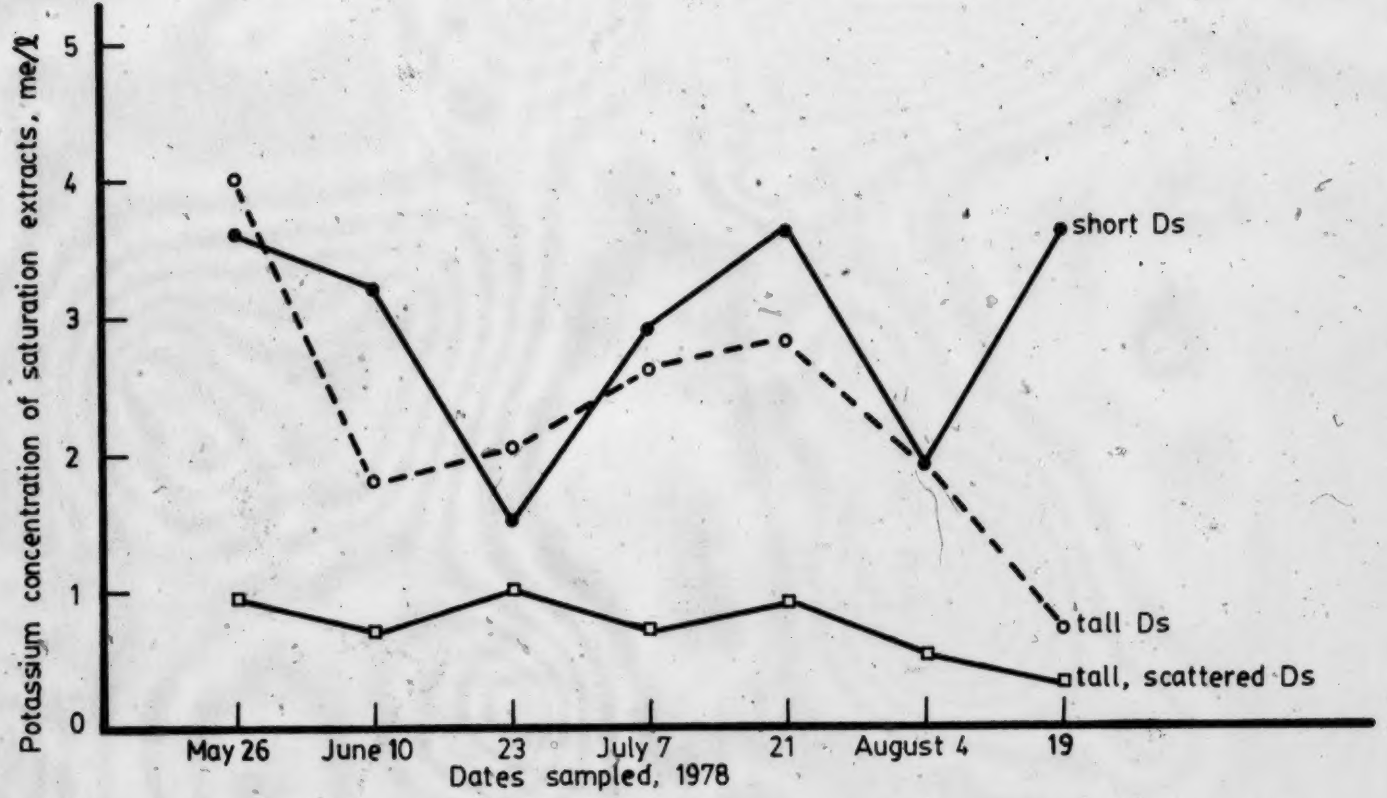

Figure 15. Potassium concentration of saturation extracts from soils of three saltgrass (Ds) zones.

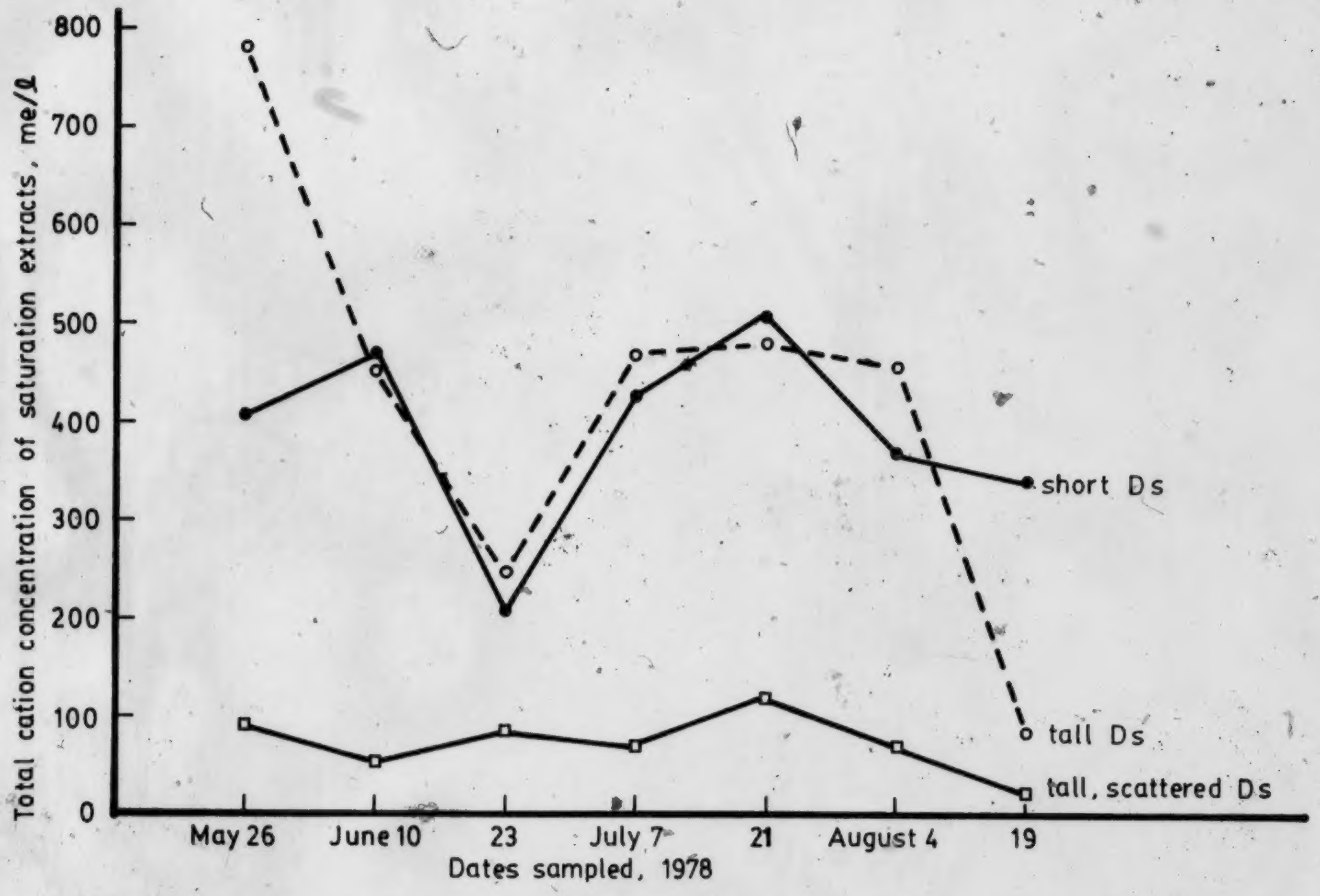

Figure 16. Total cation concentration of saturation extracts from soils of three saltgrass (Ds) zones.

in spring, lower until late June, high in mid-July, and lower through August. These soil cation levels are related to rainfall patterns. There was little rain in early May, heavy rain at the end of May and in mid-June, little rain from late June to early August, and very heavy rain in mid-August. Saturation extracts from the tall, scattered Ds soil samples had much lower cation concentrations and less pronounced fluctuations than did extracts from the other two soil zones.

The electrical conductivity of saturation extracts (ECe) from short and tall Ds soil samples (Figure 11) indicated that there were high salt concentrations in these soils. Subsequent cation analyses verified this observation. While calcium concentrations were fairly low (Figure 12), magnesium (Figure 13) and sodium (Figure 14) concentrations were much higher. Potassium concentrations (Figure 15) were extremely low compared to sodium concentrations. Total cation concentration (Figure 16) averaged about 400 me/l for short and tall Ds zones and about 75 me/l for the tall, scattered Ds zone.

The average Mg/Ca ratios (Figure 17) of the short and tall Ds zones were quite high (4 to 5) while that of the tall, scattered Ds zone was fairly low (2). The cation to total cation concentration ratios for the three zones (Figures 18 to 20) clearly indicate the relationships among the cations. Sodium and magnesium dominated; during the field season they accounted for about 90% of the cation

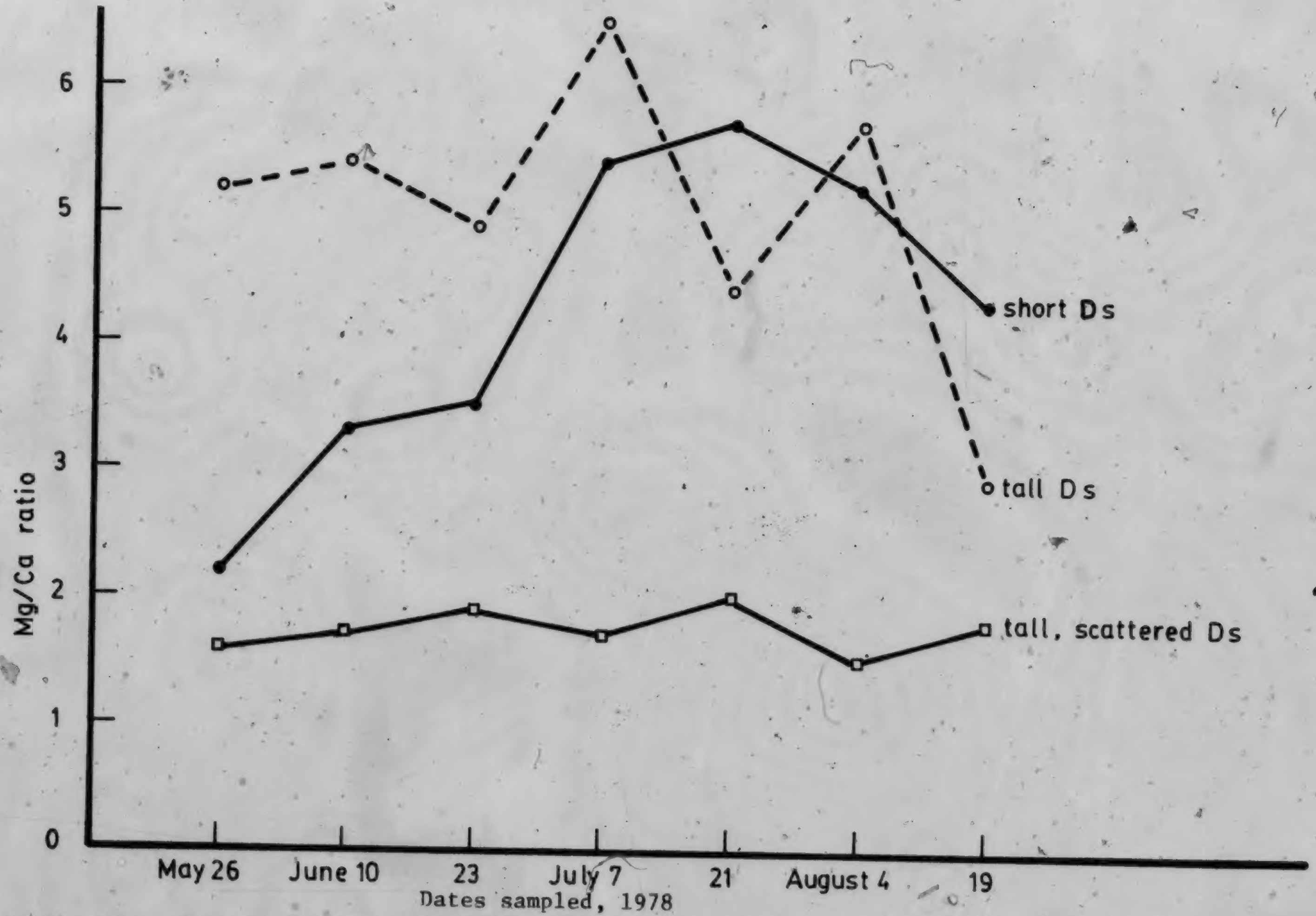

Figure 17. Magnesium to calcium ratio of saturation extracts from soils of three saltgrass (Ds) zones.

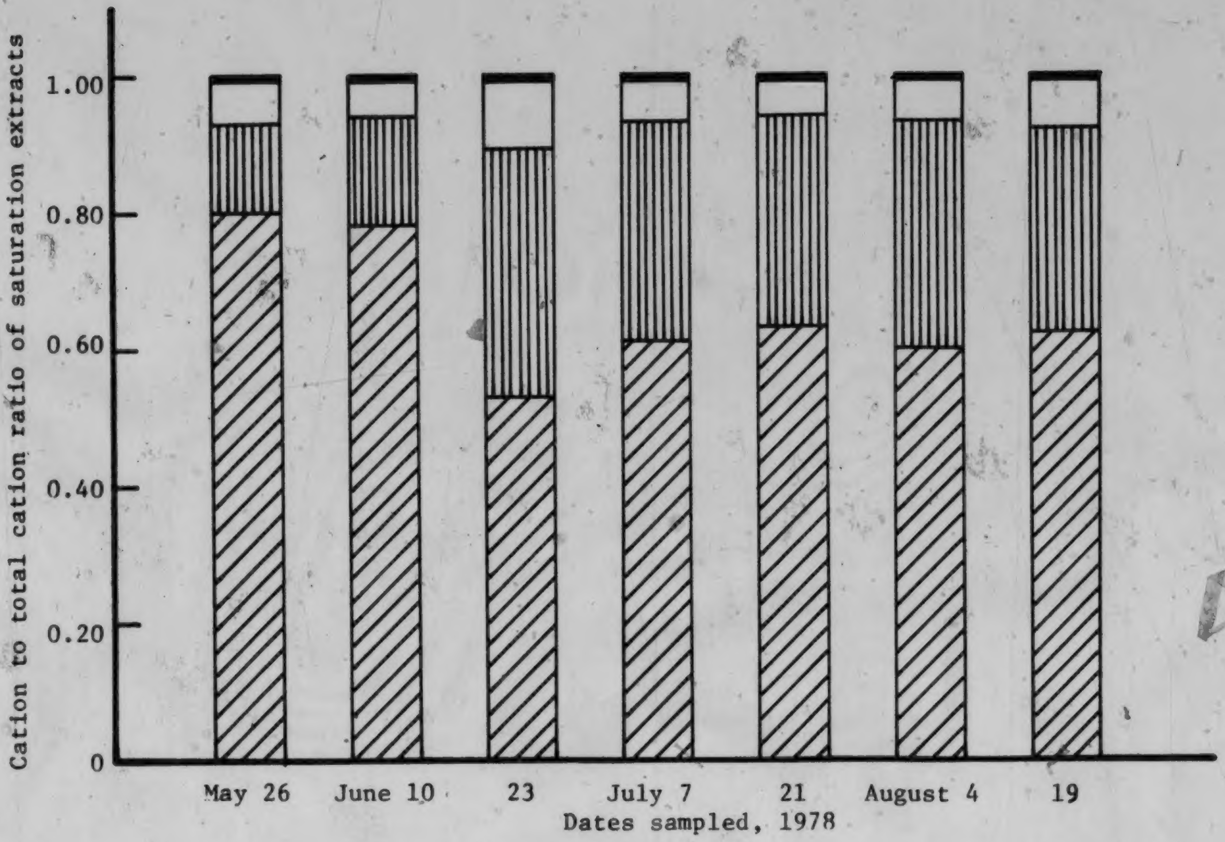

Figure 18. Cation to total cation concentration ratios of saturation extracts from soil of short Ds zone. Na/TC ▨ , Mg/TC ▥ , Ca/TC ☐ , K/TC ■ .

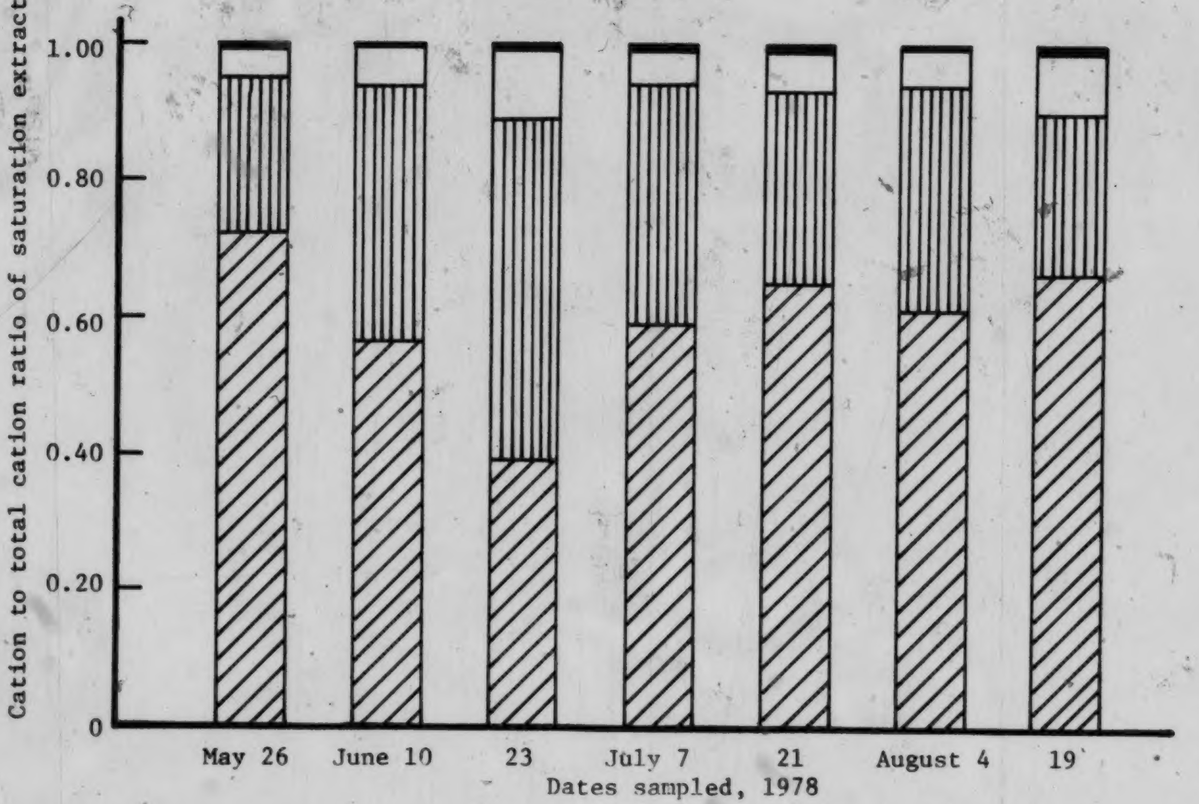

Figure 19. Cation to total cation concentration ratios of saturation extracts from soil of tall Ds zone. Na/TC ▨, Mg/TC ▥, Ca/TC ☐, K/TC ■.

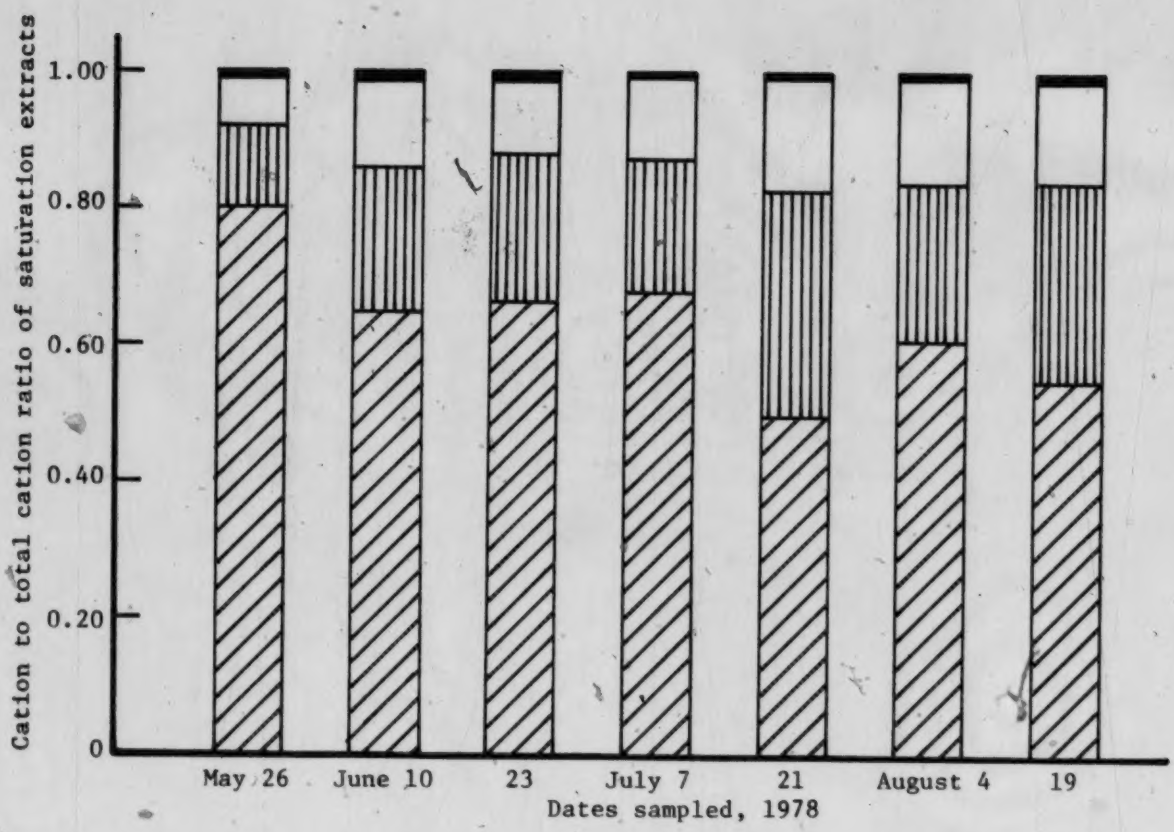

Figure 20. Cation to total cation concentration ratios of saturation extracts from soil of tall scattered Ds zone. Na/TC ▨, Mg/TC ▥, Ca/TC ☐, K/TC ■.

concentration of the saturation extracts. The proportion of potassium in the extracts was very low -- about 1%. Calcium, which was also present in low proportions, brought the total to 100%. The most noticeable difference among the three zones was in the Ca/TC ratio, which was considerably higher for the tall, scattered Ds zone than for the short and tall Ds zones.

The sodium adsorption ratios (SAR) for the short and tall Ds soil zones follow the cation concentration pattern described earlier. The values for all three zones show the dominance of sodium in these soils (Figure 21).

Results of chemical analyses of Akasu Lake water samples are presented in Table 5. The electrical conductivities and total cation concentrations of the samples were much lower than those for soil saturation extracts, but patterns similar to those in the extracts can be seen in the lake water cation ratios. Sodium and magnesium accounted for 90 to 96% of the total cation concentration. Calcium and potassium were present in low concentrations and proportions of the total cation content.

The relationship between total cation concentration and electrical conductivity of water samples and soil saturation extracts was strong, as shown by a correlation coefficient of 0.938.

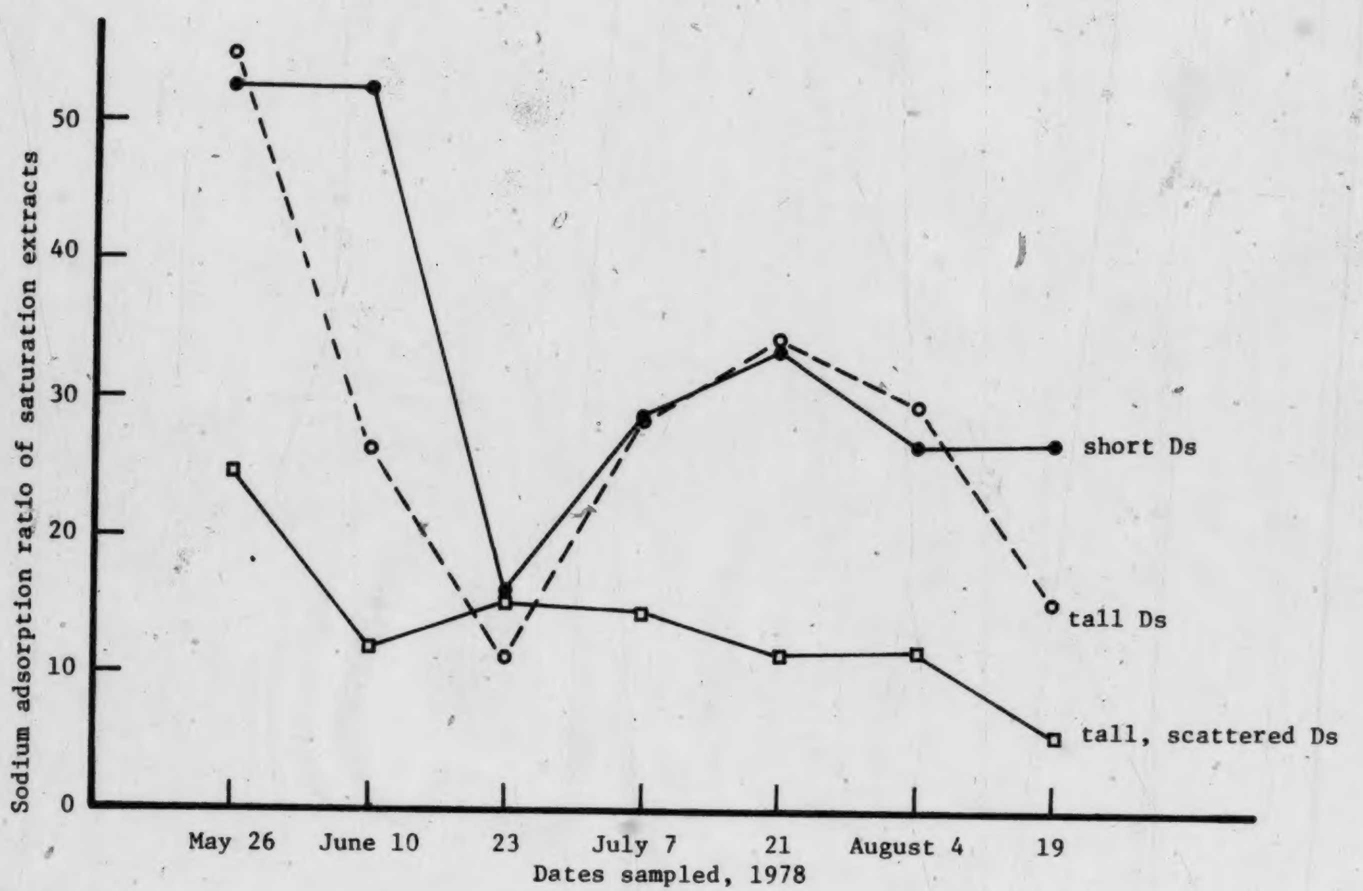

Figure 21. Sodium adsorption ratio (SAR) of saturation extracts from soils of three saltgrass (Ds) zones.

Table 5. Chemical analyses of 1978 water samples from Akasu Lake. TC = total cation concentration. EC = electrical conductivity, mS/cm.

	Sampling Dates				
	June 2	June 23	July 7	July 28	August 26
Cations			Concentrations (me/l)		
Ca	1.9	1.7	1.1	1.8	1.4
Mg	4.5	4.5	4.7	5.0	4.7
Na	37.0	37.0	31.8	31.8	31.8
K	1.3	0.8	0.7	1.0	0.9
TC	44.7	44.0	38.3	39.6	47.0
Cation ratios			Concentration ratios		
Mg/Ca	2.4	2.6	4.3	2.8	3.4
Ca/TC	0.04	0.04	0.03	0.05	0.03
Mg/TC	0.10	0.10	0.12	0.13	0.10
Na/TC	0.82	0.84	0.84	0.79	0.85
K/TC	0.03	0.02	0.02	0.02	0.02
EC	3.77	3.93	4.00	4.08	4.08
pH	8.6	8.7	8.9	8.9	8.8

4.2 Community Characterization

4.2.1 Description of species present

A list of plant species collected at Akasu Lake in the vicinity of the *Distichlis stricta* community is presented in Table 6. The twenty-one species represent ten families, of which the most important are Gramineae, Cyperaceae, Compositae, and Chenopodiaceae. The shore to shore transect (Figure 22) illustrates the dominance of species from these four families in and around the saltgrass community. Chemical analyses of soils from five areas of the transect show cation gradients along the transect. Cation concentrations increased from soils near shore to soils in the center of the peninsula.

4.2.2 Community sampling

The cover classes and frequencies of species present in the two cross-shaped sampling areas are presented in Tables 7 to 9. In area 1, the most frequently encountered species were *Hordeum jubatum*, *Distichlis stricta* and *Puccinellia nuttalliana*. *Hordeum* and *Distichlis* had the highest percent cover of the species present. *Puccinellia*, although widely distributed in the area, accounted for only 1 to 5% cover in the quadrats sampled. The remaining nine species present in area 1 were not evenly distributed along the four arms. Arms 1 and 3 (the north-south arms) had greater species diversity than arms 2 and 4, probably due to the more extensive moisture gradient from shore to shore

Table 6. Species in or near the *Distichlis stricta* community at Akasu Lake.

Species names	Abbreviations
Aster brachyactis	Asbr
Chenopodium glaucum spp. *salinum*	Chgl
Chenopodium spp.	Chspp
Cicuta douglasii	Cido
Crepis tectorum	Crte
Distichlis stricta	Dist
Eleocharis palustris	Elpa
Hordeum jubatum	Hoju
Juncus balticus	Juba
Poa spp.	Pospp
Potentilla anserina	Poan
Puccinellia nuttalliana	Punu
Ranunculus cymbalaria	Racy
Rumex maritimus var. *fueginus*	Ruma
Scirpus acutus	Scac
Scirpus nevadensis	Scne
Scirpus paludosus	Scpa
Senecio congestus var. *palustris*	Seco
Sonchus arvensis	Soar
Stellaria crassifolia	Stcr
Suaeda calceoliformis	Suca

TC	55	75	425	390	318
Mg/Ca	3	2	5	4	2
Ca/TC	0.06	0.13	0.07	0.06	0.09
SAR	16	14	28	34	32
ECe	7	8	35	33	19

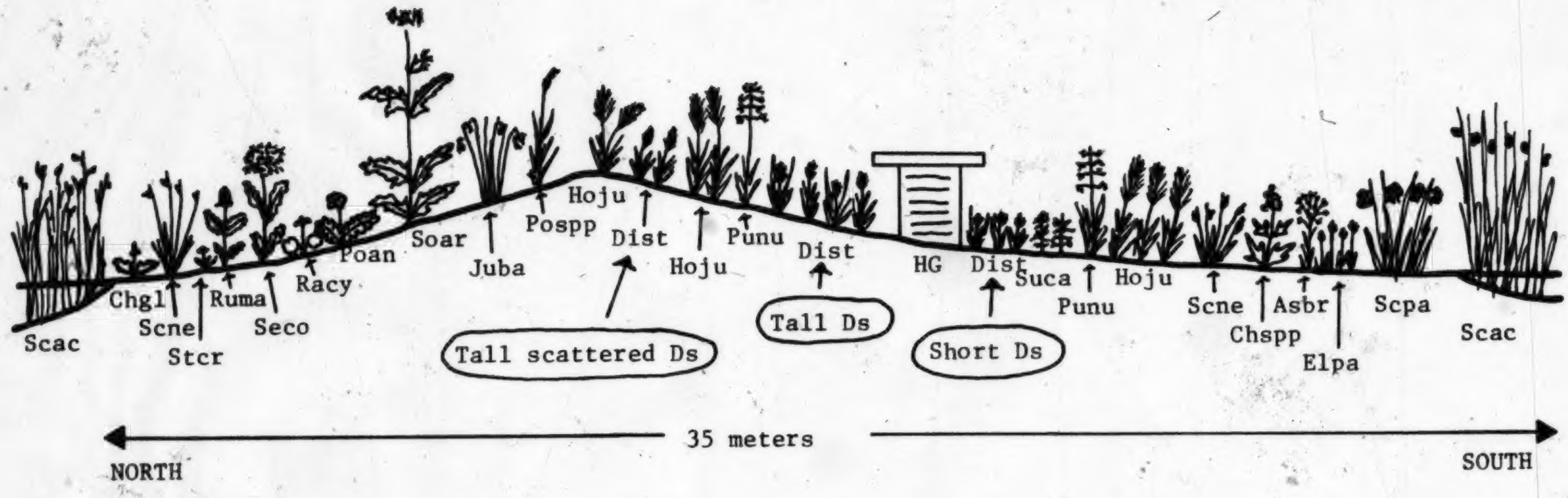
Scac
Chgl
Scne
Stcr
Ruma
Seco
Racy
Poan
Soar
Juba
Pospp
Hoju
Dist
Hoju
Punu
Dist
Tall scattered Ds
Tall Ds
HG
Dist
Suca
Punu
Hoju
Short Ds
Scne
Chspp
Asbr
Elpa
Scpa
Scac
35 meters
NORTH
SOUTH

Figure 22. Shore to shore transect through Distichlis stricta community at Akasu Lake. Names of species are abbreviated (see Table 6). Chemical characteristics of five soils are shown above the sampling locations.

Table 7. Cover classes of species in sampling area #1 at Akasu Lake. The four 16 m arms were divided into 4 m sections for which the average cover class of each species is given. The cover classes were defined as follows: 1) 1 to 5%, 2) 5 to 20%, 3) 20 to 40%, 4) 40 to 60%, 5) 60 to 80%, 6) 80 to 100%. Absence of species from sections is shown by a -. For list of species and abbreviations, see Table 6.

	Species											
	Hoju	Dist	Punu	Asbr	Scne	Chspp	Soar	Juba	Chgl	Suca	Stcr	Poan
Section	Cover Class											
Arm 1												
4 m	2	1	-	-	-	-	-	-	-	-	-	-
8 m	2	2	-	-	-	-	2	1	-	-	-	-
12 m	1	1	1	-	2	1	2	2	-	-	1	1
16 m	1	1	-	1	1	1	1	1	1	-	-	-
Arm 2												
4 m	2	4	1	-	-	-	-	-	-	-	-	-
8 m	4	2	-	-	-	-	-	-	-	-	-	-
12 m	3	2	1	-	-	-	-	-	-	-	-	-
16 m	3	1	1	-	-	-	-	-	-	-	-	-
Arm 3												
4 m	3	2	-	-	-	-	-	-	-	-	-	-
8 m	2	3	1	-	1	1	-	-	-	-	-	-
12 m	1	-	1	1	2	1	-	-	1	-	-	-
16 m	2	1	1	1	1	1	-	-	1	-	-	-
Arm 4												
4 m	3	2	-	1	-	-	-	-	-	1	-	-
8 m	2	2	-	-	-	-	-	-	-	1	-	-
12 m	2	3	1	1	-	-	-	-	-	1	-	-
16 m	2	2	1	1	-	-	1	-	-	-	-	-

Table 8. Cover classes of species in sampling area #2 at Akasu Lake. The four 16 m arms were divided into 4 m sections for which the average cover class of each species is given. The cover classes were defined as follows: 1) 1 to 5%, 2) 5 to 20%, 3) 20 to 40%, 4) 40 to 60%, 5) 60 to 80%, 6) 80 to 100%. Absence of species from sections is shown by a -. For list of species and abbreviations, see Table 6.

						Species							
	Punu	Dist	Hoju	Suca	Chspp	Asbr	Soar	Juba	Chgl	Pospp	Scne	Elpa	Cido
Section							Cover Class						
Arm 1													
4 m	1	2	1	3	1	-	-	-	-	-	-	-	-
8 m	1	1	1	4	1	-	-	-	-	-	-	-	-
12 m	-	1	2	-	1	-	2	-	-	-	-	-	-
16 m	-	-	1	-	-	-	2	2	-	1	-	-	1
Arm 2													
4 m	3	1	1	2	-	-	-	-	-	-	-	-	-
8 m	2	2	1	1	-	-	-	-	-	-	-	-	-
12 m	1	2	2	1	-	-	-	-	-	-	-	-	-
16 m	1	2	2	-	-	-	-	-	-	1	-	-	-
Arm 3													
4 m	2	1	-	2	-	-	-	-	-	-	-	-	-
8 m	2	1	2	1	1	1	-	-	-	-	-	-	-
12 m	2	1	2	1	1	1	-	-	-	-	-	1	-
16 m	2	-	1	-	1	1	-	-	1	-	1	-	-
Arm 4													
4 m	1	1	-	4	-	-	-	-	-	-	-	-	-
8 m	2	1	-	4	1	-	-	-	-	-	-	-	-
12 m	1	1	-	2	1	1	-	-	-	-	-	-	-
16 m	1	1	3	1	1	1	-	-	-	-	-	-	-

Table 9. Frequency of species in two sampling areas at Akasu Lake. Frequency is based on the percentage occurrence of each species in the 48 quadrats sampled. Area 1 included both tall and short forms of _D_. _stricta_; Area 2 included only the short form. For list of species and abbreviations, see Table 6.

Species	Frequency	
	Area 1	Area 2
Hoju	96	69
Dist	69	69
Punu	44	77
Asbr	25	23
Scne	25	4
Chspp	23	42
Soar	13	17
Juba	13	8
Chgl	10	6
Suca	10	56
Stcr	2	0
Poan	2	0
Pospp	0	6
Elpa	0	2
Cido	0	2

along arms 1 and 3.

In area 2, *Puccinellia*, *Hordeum*, *Distichlis* and *Suaeda calceoliformis* had the highest frequencies. *Suaeda* had the highest percent cover in the quadrats in which it was found. *Puccinellia* covered more ground than in area 1, while *Hordeum* and *Distichlis* (which was of the short growth form) had somewhat lower cover than in area 1. The remaining species included some which were not found in area 1.

4.2.3 Saltgrass zone transects

Only four species were present in the two 12 m transects through the saltgrass community. For transect 1, their frequencies were as follows: *Puccinellia* 100%, *Distichlis* 96%, *Hordeum* 92%, and *Aster brachyactis* 21%. For transect 2, the frequencies were *Distichlis* 100%, *Hordeum* 96%, *Puccinellia* 96%, and *Aster* 17%. Although *Aster* was present in several quadrats in both transects, it accounted for less than 1% cover where it was found. The distribution patterns of the three major species in both transects are shown in Figures 23 and 24. In both transects *Distichlis* had the highest percent cover in the short Ds zone and lowest in the tall, scattered Ds zone. Where *Distichlis* had high percent cover, *Hordeum* had low cover and vice versa. *Puccinellia* had low percent cover (under 15%) in both transects.

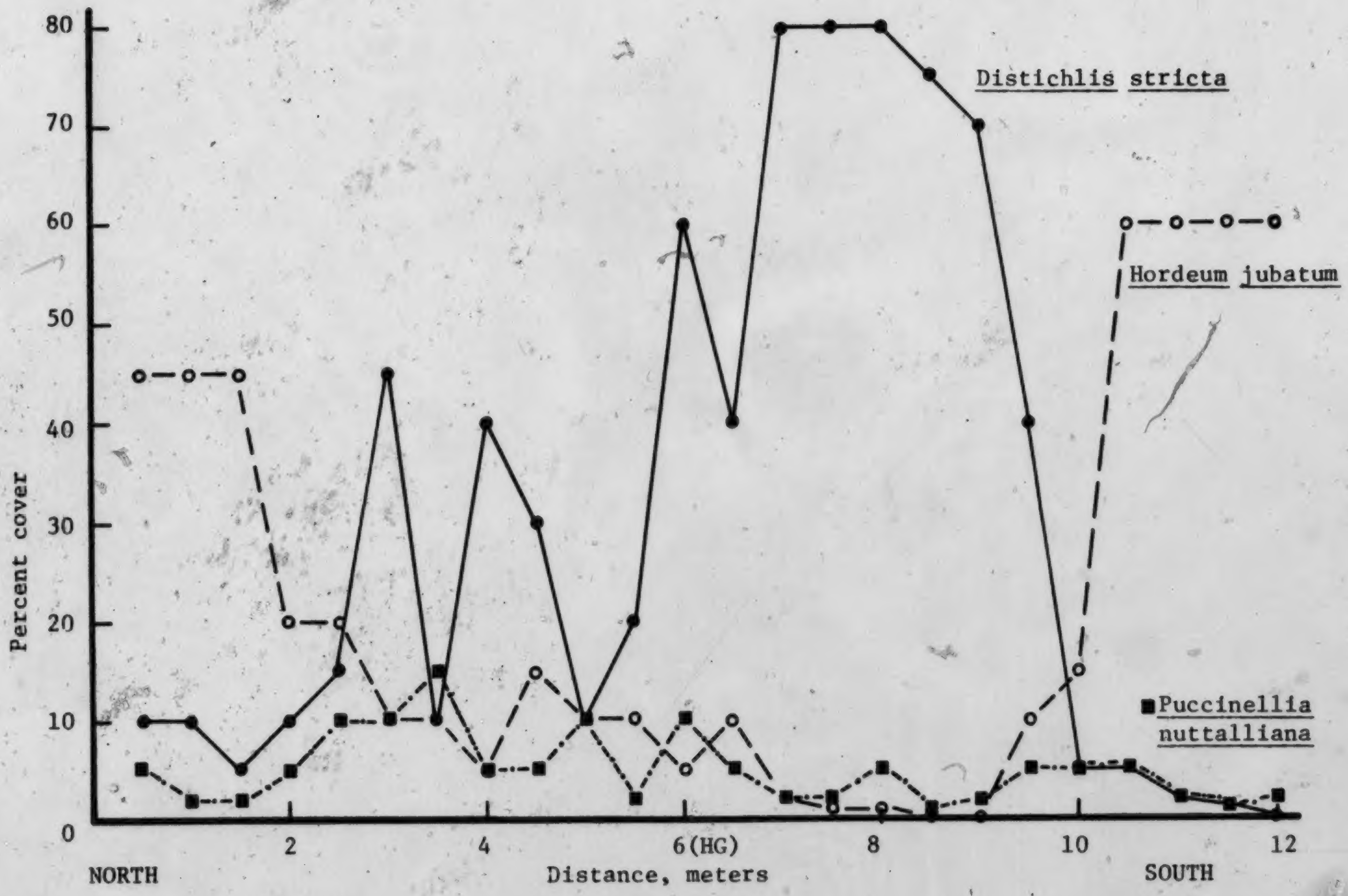

Figure 23. Percent cover of species along Transect 1. The tall, scattered Ds zone extended from 0 to 3 m, tall Ds from 3 to 6 m, and short Ds from 6 to 10 m. For soil salinity relationships, see Figures 11 and 16.

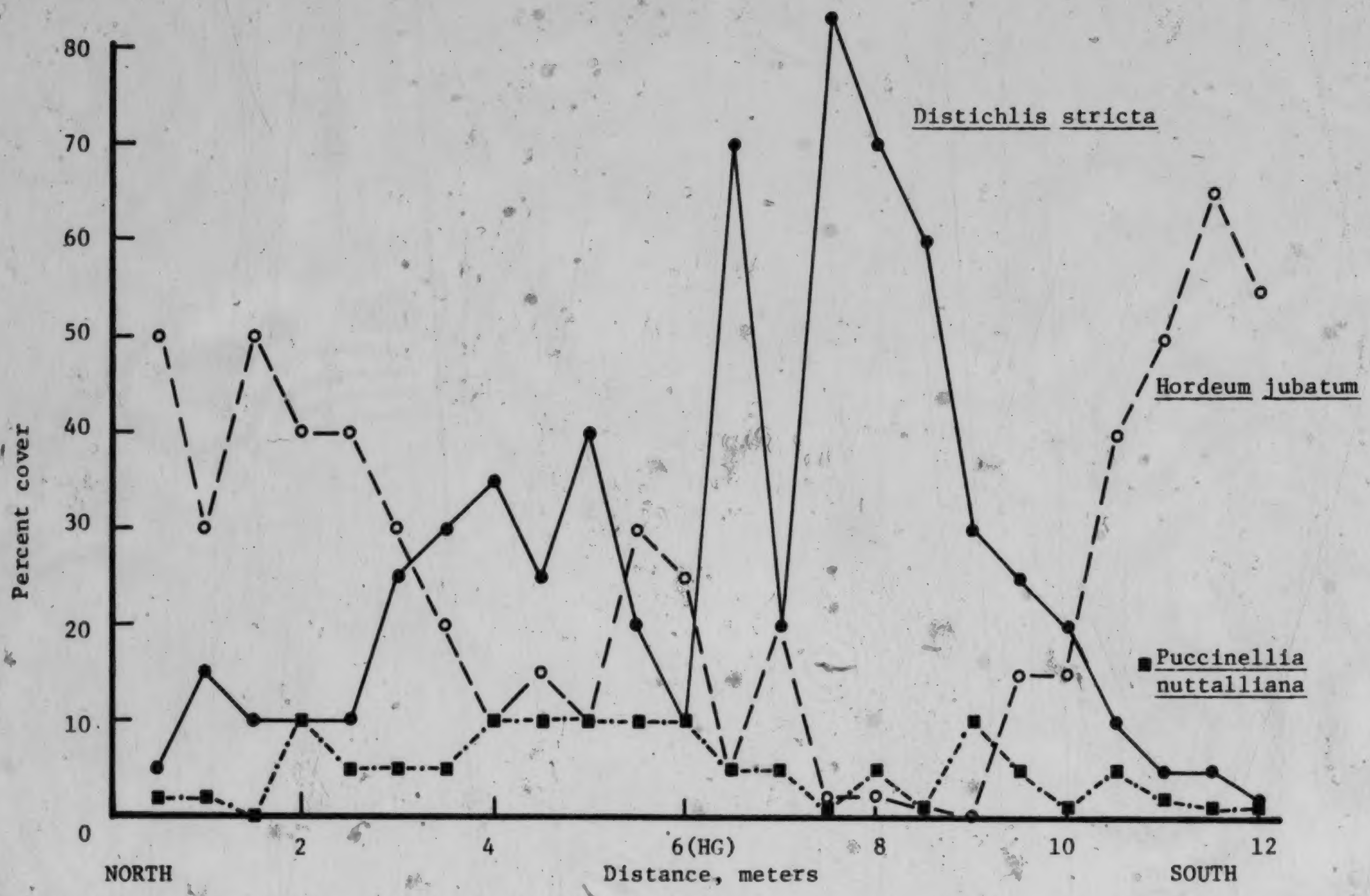

Figure 24. Percent cover of species along Transect 2. The tall, scattered Ds zone extended from 0 to 3 m, tall Ds from 3 to 6 m, and short Ds from 6 to 10 m. For soil salinity relationships, see Figures 11 and 16.

4.3 Growth of saltgrass in the field

4.3.1 Phenological observations

Distichlis stricta broke dormancy in early to mid-May and began to flower in late May to early June. Male flowers generally appeared first, but they were soon followed by female flowers. By mid-July, growth was very slow and few new flowering panicles appeared. By the end of August most plants were dormant.

Throughout the summer, rhizomatous growth occurred, with new shoots appearing at various distances from the original plant. This vegetative growth seemed to be the primary means by which saltgrass spread. The coarse, branching rhizomes were found in the top 5 to 10 cm of soil and were often several decimeters long. The coarse to fine roots extending from the rhizomes through the soil were concentrated in the top 15 cm, although many penetrated more deeply.

4.3.2 Shoot growth

The increase in height of tagged short and tall saltgrass shoots is presented in Figure 25 with the corresponding weekly soil moisture percentages. Statistical analysis (Appendix 1) confirmed that the tall shoots were significantly larger ($p<0.01$) than the short shoots during the entire observation period. The average height of the short plants increased from 4 to 7 cm, while that of the tall plants increased from 5 to 9 cm over the seven week

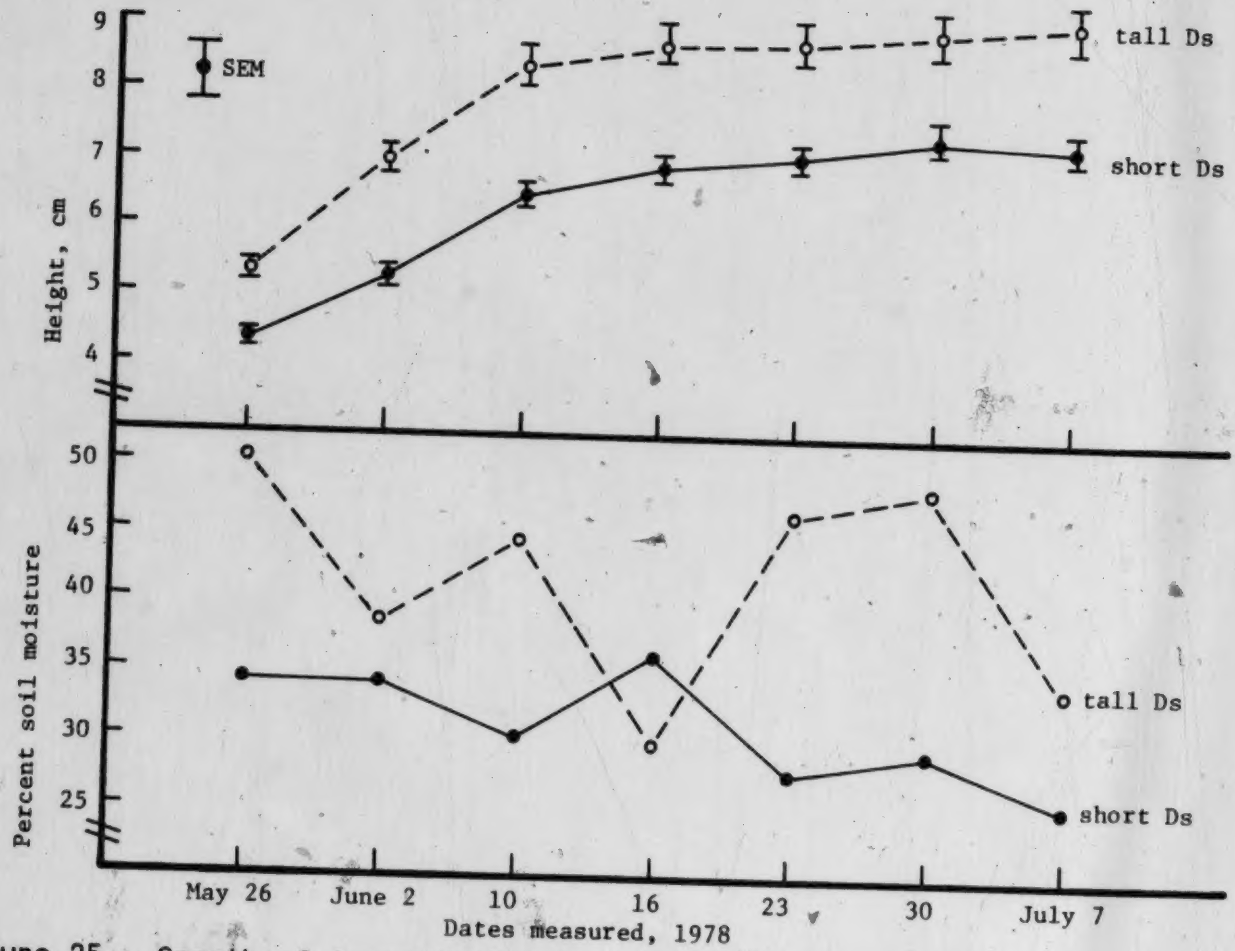

Figure 25. Growth of tagged saltgrass shoots (upper graph) and corresponding soil moisture levels at Akasu Lake.

period.

4.3.3 Flowering percentage

There were no significant differences in total or male flowering percentages between short and tall saltgrass in 1977 and 1978 (Table 10 and Appendix 2). In 1978 there were significantly more female flowers in the short than in the tall saltgrass quadrats. This difference may have been due to the rhizomatous nature of saltgrass, which results in uneven distribution of male and female plants. Quadrats may therefore contain large proportions of one or the other sex. The total flowering percentage, a more reliable parameter, averaged from 17 to 18% for both growth forms in 1977 and 1978.

4.4 Solution Culture Studies

4.4.1 Experiment 1

4.4.1.1 Growth of plants

Saltgrass plants at all four Mg/Ca ratios grew rapidly and appeared healthy for the duration of the experiment (Plate 4). Growth data are presented in Table 11. There were no significant differences in number of shoots, shoot height or dry weight between treatments (Appendix 3). The number of shoots increased from the original number (7) by factors of four (treatment 3), five (treatment 2), six (treatment 1), and seven (treatment 4) due to rhizome growth and sprouting. Mean shoot height, which was initially 6 cm,

Table 10. Flowering percentages of short and tall *Distichlis stricta* in 1977 and 1978. Values given are means (plus or minus SEM) of five quadrats sampled for each growth form.

Category and year	Short *D. stricta*	Tall *D. stricta*
	Flowering Percentage	
% male flowers		
1977	9.9 ± 5.6	14.7 ± 5.3
1978	6.5 ± 0.6	13.0 ± 4.2
%female flowers		
1977	8.4 ± 2.6	2.7 ± 1.2
1978	11.0 ± 2.0	3.6 ± 1.4
% total flowers		
1977	18.3 ± 5.3	17.4 ± 5.3
1978	17.4 ± 1.5	16.6 ± 3.4
	Total Shoots	
1977	74 ± 7	149 ± 43
1978	199 ± 21	168 ± 17

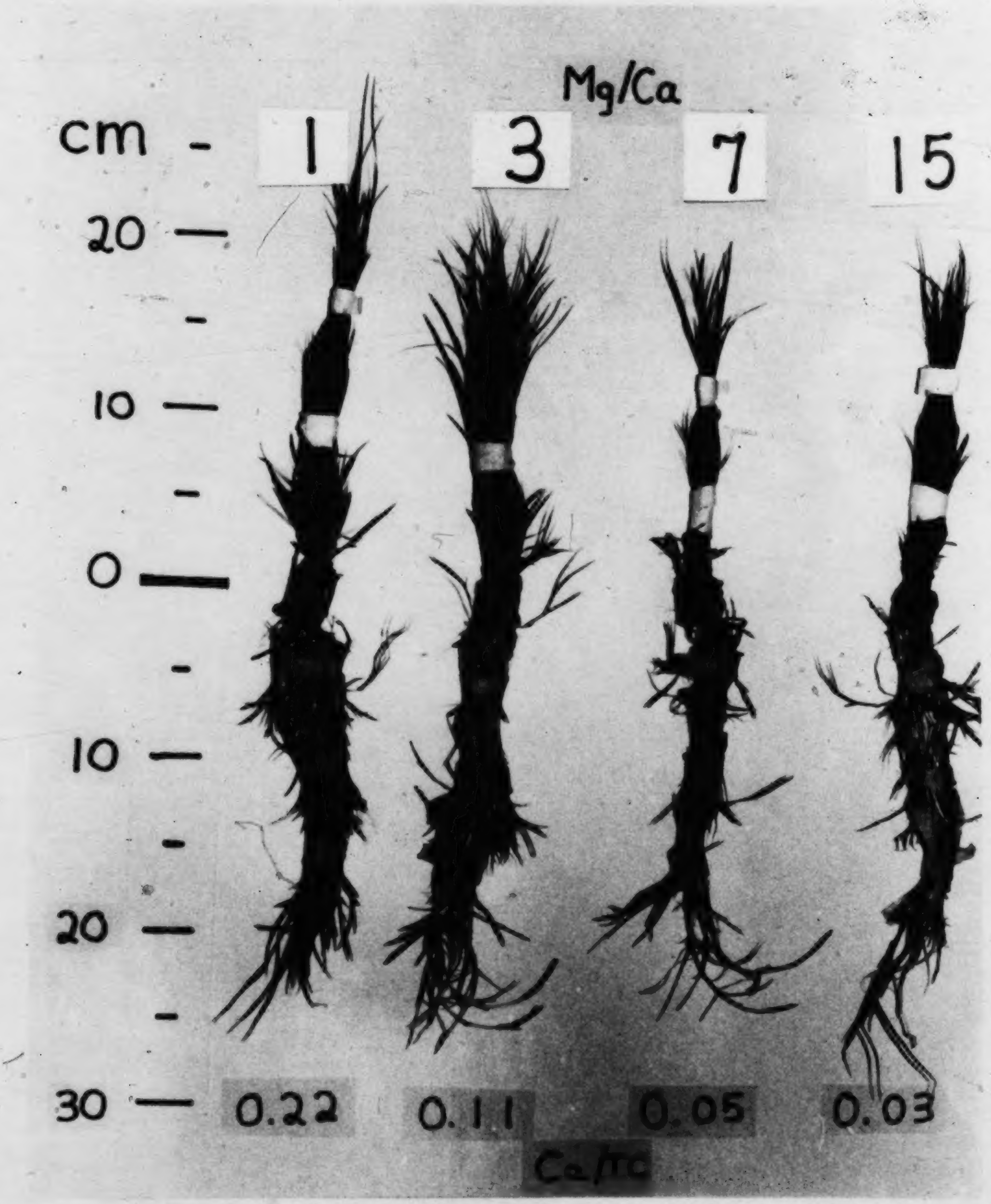
Mg/Ca
cm
1
3
7
15
20
10
0
10
20
30
0.22
0.11
0.05
0.03
Ca/TC

Plate 4: Effect of increasing Mg/Ca and decreasing Ca/TC on growth of saltgrass in Experiment 1.

Table 11. Saltgrass growth data for solution culture Experiment 1. All measurements were recorded after six weeks of growth. The values given are means (plus or minus SEM) of three replicates for each treatment.

Treatment	Solution Mg/Ca	Number of shoots	Shoot height (cm)	Dry weight (gm)	
				Shoot	Root
1	1	41 ± 3	13.7 ± 1.5	1.86 ± 0.24	1.78 ± 0.33
2	3	36 ± 13	13.3 ± 0.9	1.85 ± 0.61	1.94 ± 0.36
3	7	29 ± 5	11.0 ± 0	1.07 ± 0.19	1.12 ± 0.05
4	15	51 ± 8	13.0 ± 0.6	1.94 ± 0.32	1.50 ± 0.18

ranged from 11 to 14 cm after six weeks for the four treatments. Treatments 1, 2 and 4 had fairly close shoot and root dry weights, but treatment 3 had considerably lower dry weight. There were flowering shoots present in all treatments except treatment 3. This experiment showed that saltgrass plants were able to grow in solutions with a wide range of Mg/Ca with little effect on physical properties of most plants.

4.4.1.2 Tissue analyses

Raw data and statistical analyses of cation concentrations and ratios are presented in Appendices 4 and 5. Tissue calcium concentration tended to decrease as solution calcium concentration decreased (Figure 26), but not in the same proportions. There were no significant differences in shoot calcium concentrations between groups, but regressions of shoot calcium on solution calcium and on solution Mg/Ca were significant. Treatments 1 and 4 differed significantly with respect to root calcium concentration. The regressions of root calcium on solution calcium and on solution Mg/Ca were significant at $p < 0.01$.

Tissue magnesium levels tended to increase as solution levels increased (Figure 27). There were no significant results shown by ANOV and regression analysis on shoot data, but regressions of root magnesium concentration on solution magnesium and on solution Mg/Ca were significant. Root tissue from treatments 3 and 4 had

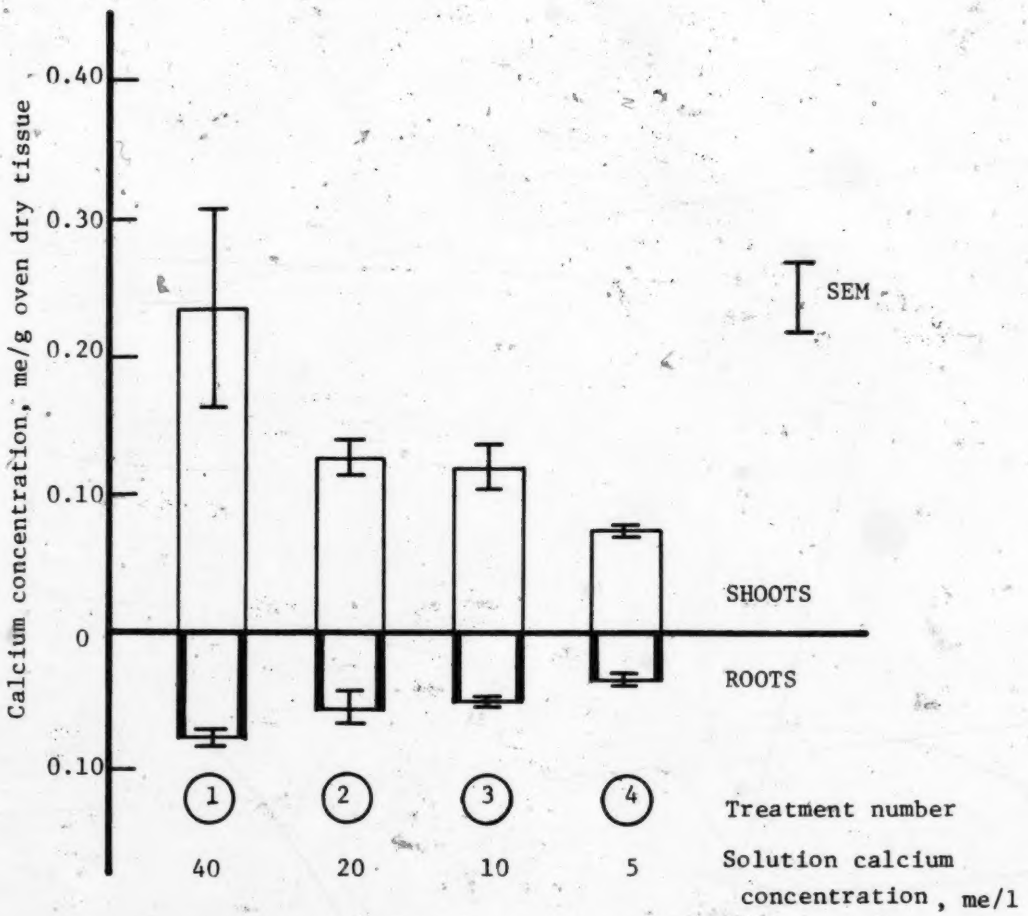

Figure 26. Mean calcium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1).

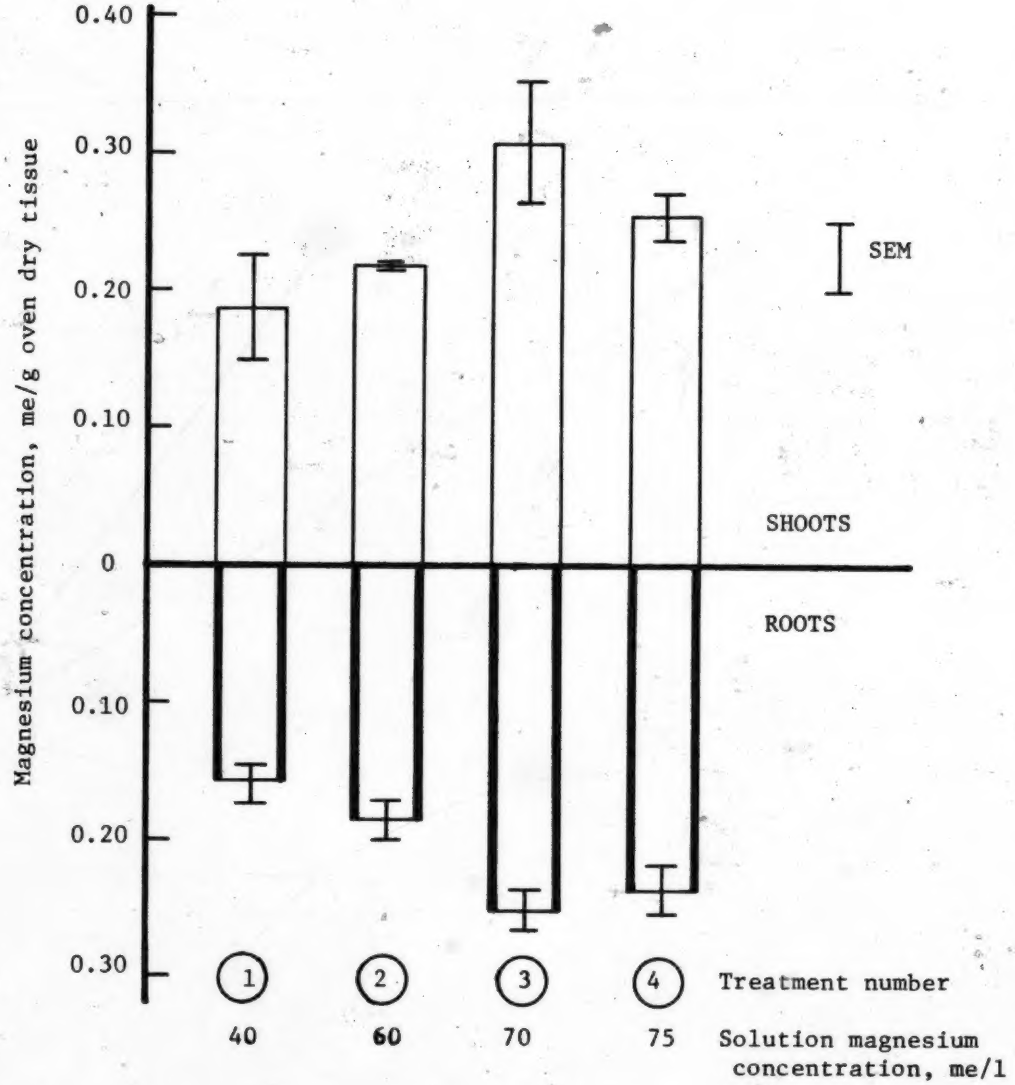

Figure 27. Mean magnesium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1).

significantly higher magnesium concentrations than did root tissue from treatment 1.

Shoot sodium levels were similar for all treatments. Root levels increased slightly but not significantly as solution calcium levels decreased (Figure 28). Tissue potassium concentrations were by far the highest of the cations (Figure 29). Shoot concentrations of all treatments were similar, except for group 2, while root concentrations were similar except for group 3. Although there was a fair amount of variation in total cation concentration (Figure 30), there was no consistent pattern in shoot and root levels and there were no significant differences between groups.

The Mg/Ca ratios in saltgrass tissue were significantly affected by solution Mg/Ca ratios (Figure 31, Appendix 5). As Mg/Ca increased in solution, it also increased in plant tissue but in much lower proportions. Shoot Mg/Ca ratios were considerably lower than corresponding root ratios. Regressions of solution Mg/Ca on tissue Mg/Ca were significant at $p<0.01$.

A comparison of solution and tissue cation to total cation concentration ratios is presented in Figure 32. The most striking difference was found between potassium to total cation concentration (K/TC) in solution and K/TC in plant tissue for all treatments. The plants in all four solutions selectively absorbed potassium so that similar K/TC ratios were attained by all plants. The Na/TC ratio

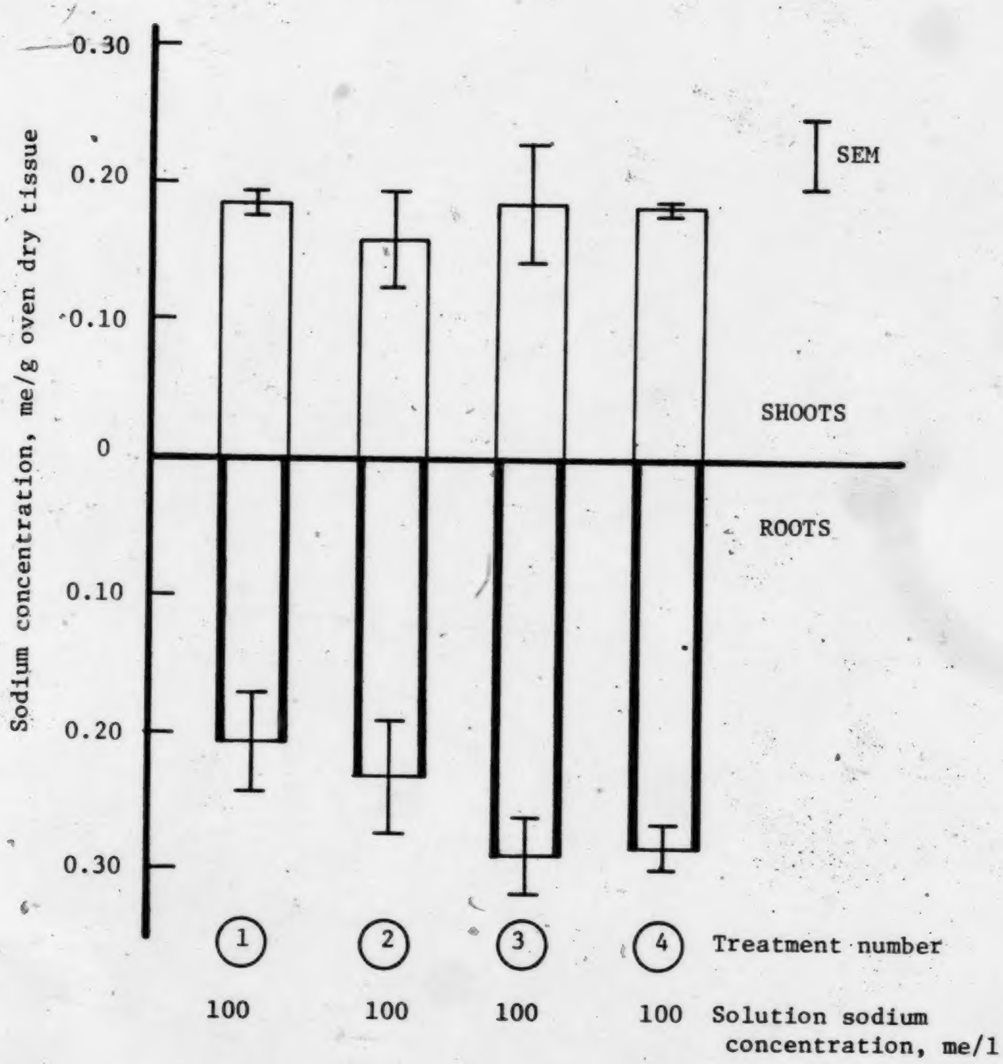

Figure 28. Mean sodium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1).

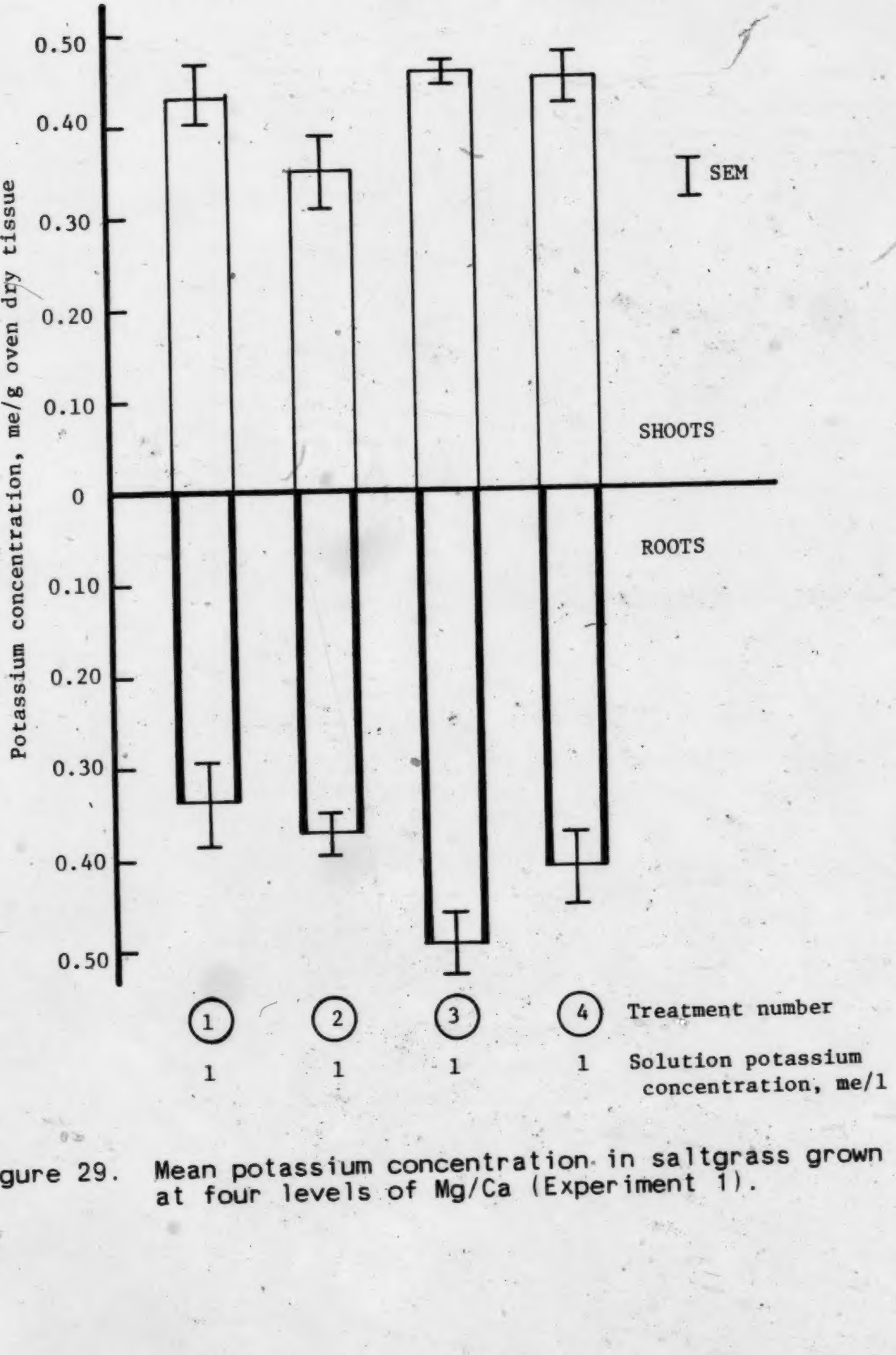

Figure 29. Mean potassium concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1).

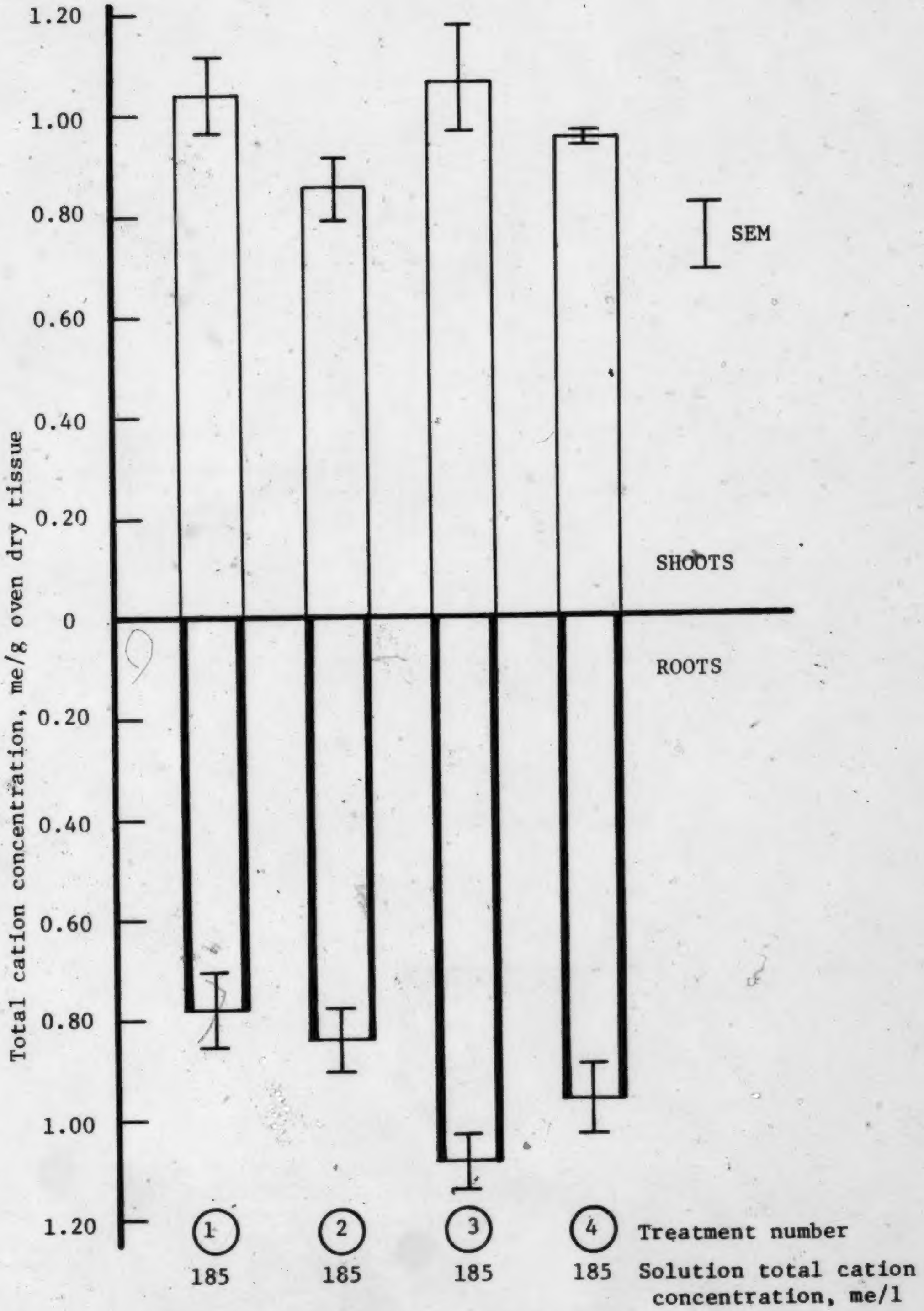

Figure 30. Mean total cation concentration in saltgrass grown at four levels of Mg/Ca (Experiment 1).

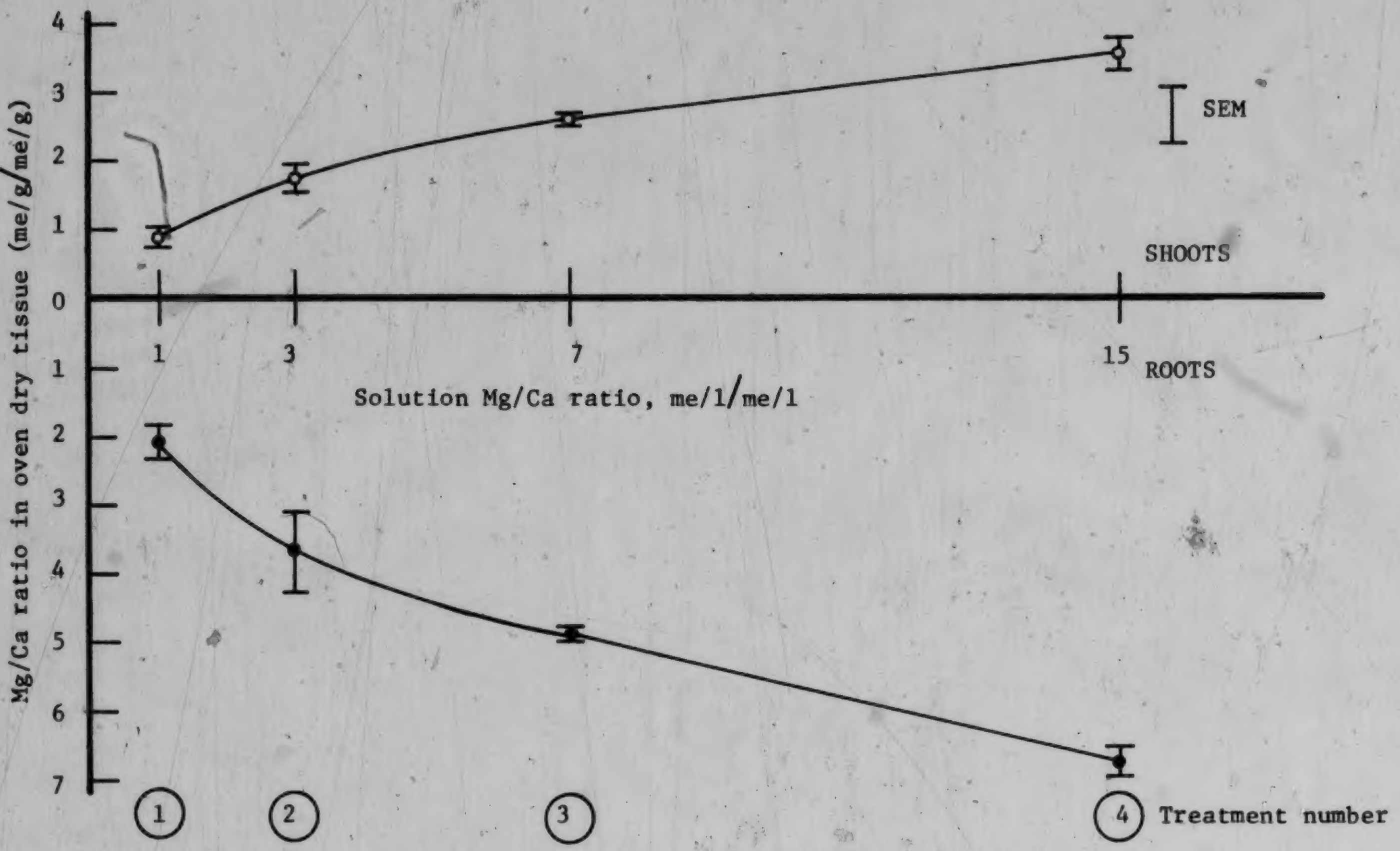

Figure 31. Mean tissue Mg/Ca vs. solution Mg/Ca ratio for saltgrass grown at four levels of Mg/Ca (Experiment 1).

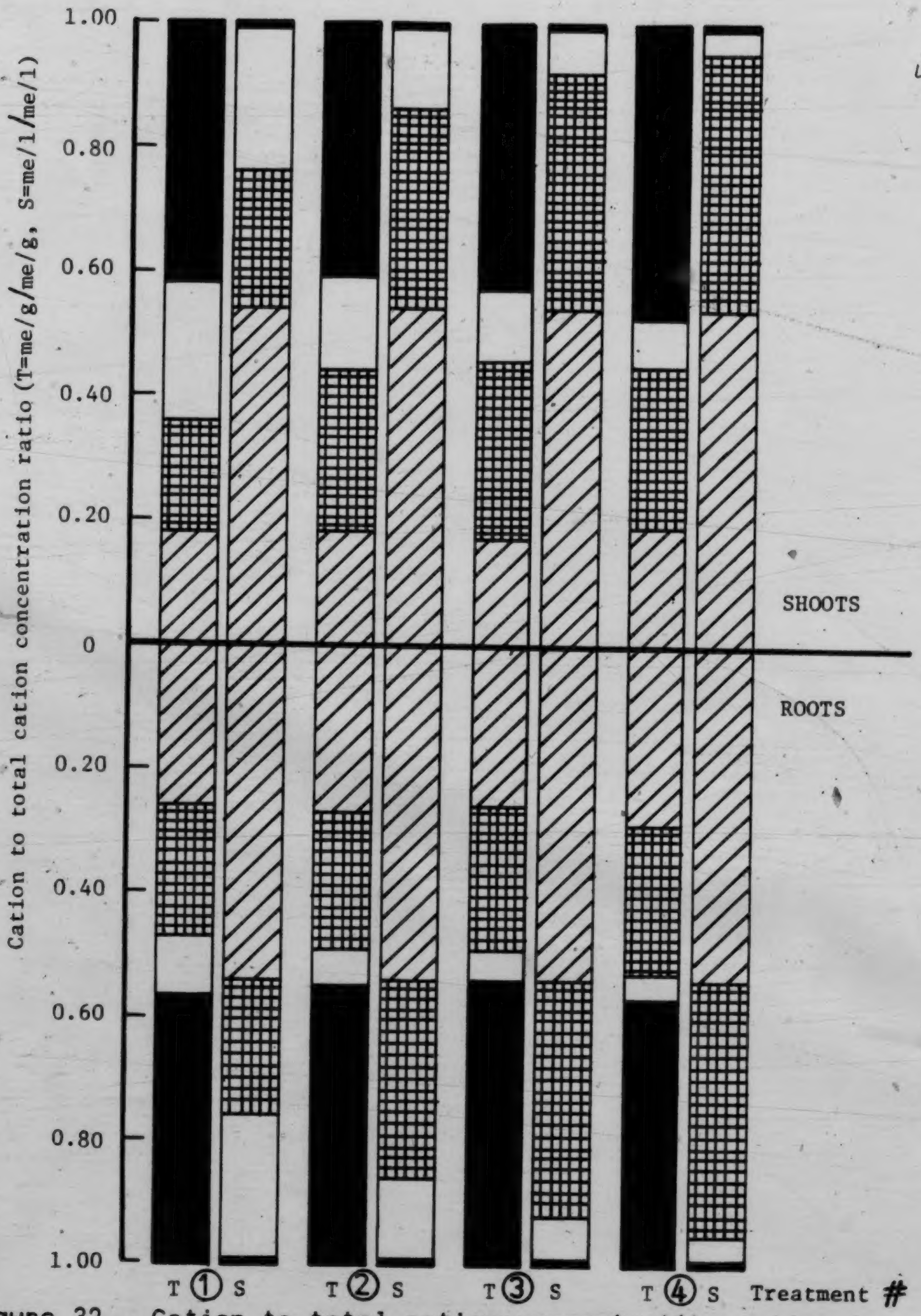

Figure 32. Cation to total cation concentration ratios in tissue vs. solutions for saltgrass grown at four levels of Mg/Ca (Experiment 1). Na/TC ▨, Mg/TC ▦, Ca/TC ▭, K/TC ■. Tissue = T, solution = S.

also differed greatly from solution to plant tissue. In this case plants in all groups excluded sodium. The Mg/TC ratio in plant tissue increased somewhat as solution Mg/TC increased. Treatment 3 shoot tissue had a significantly larger Mg/TC ratio than did shoot tissue in treatment 1. The increases in Mg/TC in root tissue of the four treatments were not as large as for shoot tissue; there were no significant differences between groups. The Ca/TC ratio in shoot tissue decreased considerably as solution Ca/TC decreased (shoot Ca/TC of group 1 was three times that of group 4), but the differences were not significant. However, a regression of shoot Ca/TC on solution Mg/Ca was significant at $p<0.05$. Root Ca/TC decreased considerably from treatment 1 to 4. There were significant differences between groups 1 and 3, and 1 and 4, and a regression of root Ca/TC on solution Mg/Ca was significant at $p<0.01$.

The results of the test for correlations between dry weight and cation concentrations and ratios are presented in Appendix 6. Shoot dry weight was not significantly correlated with any of the cation variables. However, there were significant correlations ($p<0.05$) between root dry weight and magnesium, potassium, and total cation concentrations.

The results of Experiment 1 indicate that changing the calcium and magnesium concentrations and ratios in culture solutions did not significantly affect growth and external appearance of saltgrass plants, but did significantly affect some of the tissue cation concentrations and ratios. Internal concentrations of calcium and magnesium tended to increase or decrease in the same direction as solution concentrations, but not in the same proportions. Tissue levels of potassium were relatively high, and levels of sodium were relatively low at all treatment levels.

4.4.2 Experiment 2

4.4.2.1 Growth of plants

The two Mg/Ca ratios and three levels of sodium sulfate used in this experiment had inconsistent effects on plant growth. Saltgrass and barley plants are shown at two weeks in Plate 5 and at eight weeks in Plate 6. There was considerable variation in survival and growth of saltgrass both within treatments and among treatments. All plants in replicates 1 and 2 of treatment A3 and all plants in treatment B3 died well before the end of the experiment. In some of the other treatment replicates, several of the original ten plants died and were not completely replaced by new shoots produced by the rhizomes. This happened in treatments A1, A2, B2 and C. In other treatments, although several of the original plants died, rhizome sprouting and tillering produced several new shoots which brought shoot totals to as high as 43 (treatment A1, replicate 4). In every replicate at least one of the original ten plants died.

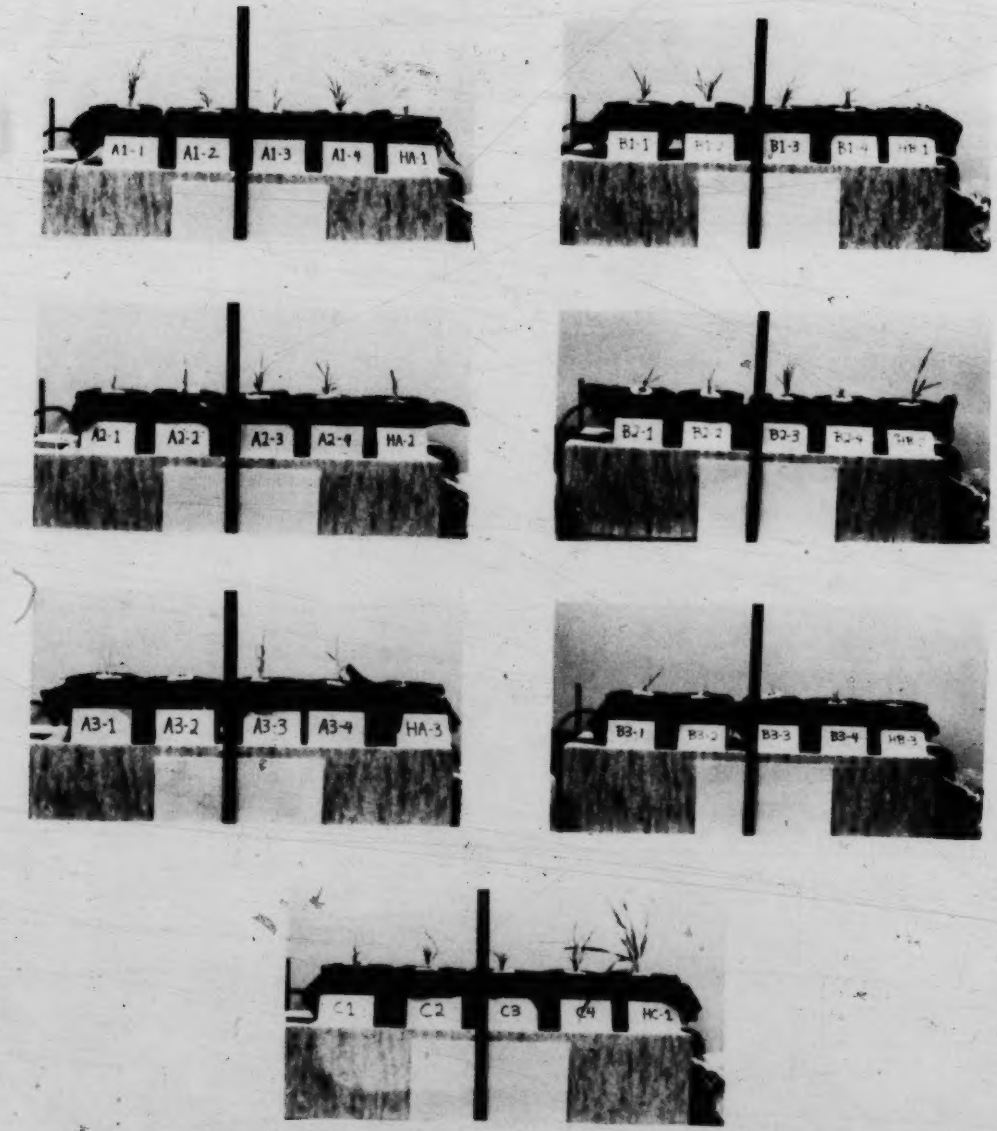
A1-1
A1-2
A1-3
A1-4
HA-1
B1-1
B1-2
B1-3
B1-4
HB-1
A2-1
A2-2
A2-3
A2-4
HA-2
B2-1
B2-2
B2-3
B2-4
A3-1
A3-2
A3-3
A3-4
HA-3
B3-1
B3-2
B3-3
B3-4
HB-3
C1
C2
C3
C4
HC-1

Plate 5: Growth of saltgrass at two weeks in Experiment 2. Mg/Ca was 5 in A, 1 in B, and 0.25 in C. [Na] was 0 in C, 50 in A1 and B1, 100 in A2 and B2, and 300 me/l in A3 and B3. 'H' refers to Hordeum.

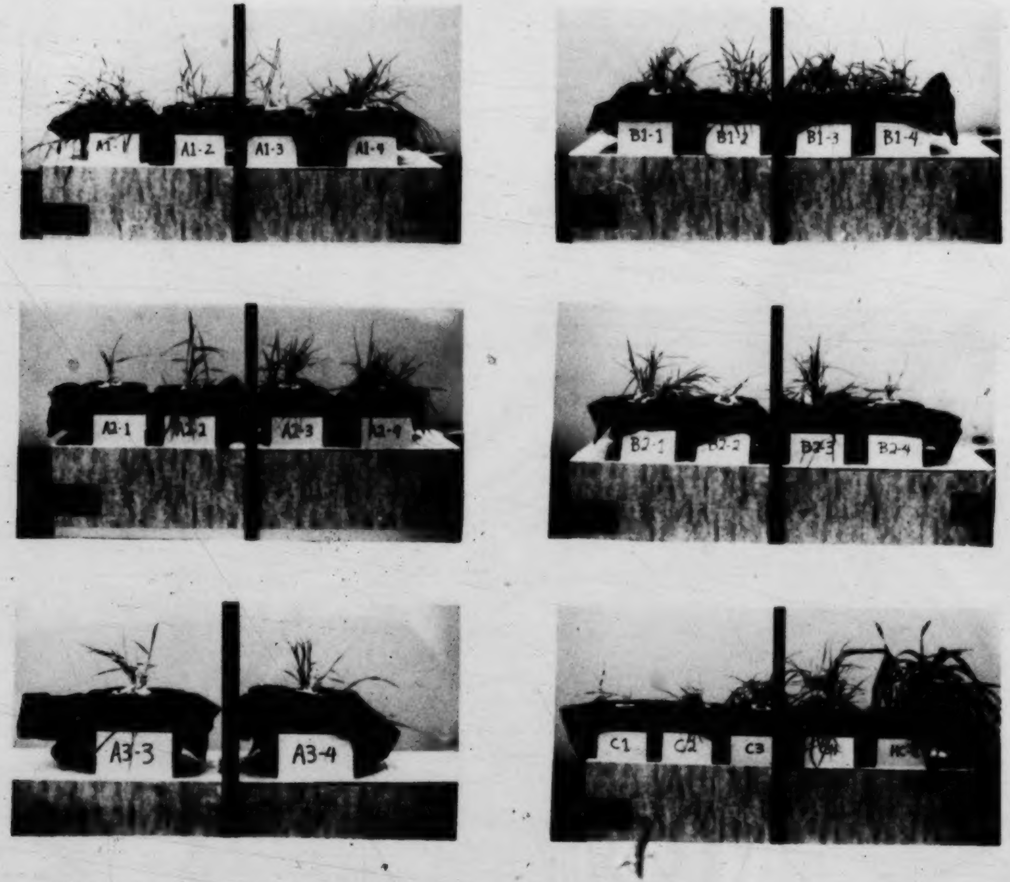
A1-1
A1-2
A1-3
A1-4
B1-1
B1-2
B1-3
B1-4
A2-1
A2-2
A2-3
A2-4
B2-1
B2-2
B2-3
B2-4
A3-3
A3-4
C1
C2
C3

Plate 6: Growth of saltgrass at eight weeks in Experiment 2. Mg/Ca was 5 in A, 1 in B, and 0.25 in C. [Na] was 0 in C, 50 in A1 and B1, 100 in A2 and B2, and 300 me/l in A3. 'H' refers to Hordeum.

Growth variables (number of shoots, height, water content, fresh and dry weights) for saltgrass plants are presented in Table 12. The two replicates which died were not included in any of the calculations for treatment A3. The values given for this treatment are means of the two surviving replicates. Since all plants in treatment B3 died, recording of growth variables (except for dry weight) was not possible.

Although all growth variables tended to decrease in value from treatment 1 (50 me/l Na) to treatment 3 (300 me/l Na), there were no significant differences between any of the groups (Appendix 7). Control plants had lower values of growth variables than plants in treatments A1 and B1 but the differences were not significant.

By the fourth week of the experiment, all barley plants had died except those in the control treatment. Growth data for the dead plants, which were separated into shoots and roots, are presented in Appendix 8. All dead plants had very low dry weights. There were no consistent patterns of difference shown among the dead treatments.

4.4.2.2 Water potential measurements

The results of pressure bomb readings of saltgrass water potentials are presented in Figure 33 (for raw data and statistics see Appendix 9). The high water potential (-507 kPa) of treatment C was significantly different from that of all the other groups except B1. The lowest water

Table 12. Saltgrass growth data for solution culture Experiment 2. All measurements were recorded after eight weeks of growth. The values given are means (plus or minus SEM) of four replicates for each treatment except A3, in which two replicates were used. Treatment symbols refer to Mg/Ca ratio and salt concentration. A refers to Mg/Ca = 5, B refers to Mg/Ca = 1, C = control (no added sodium), 1 = 50 me/l Na, 2 = 100 me/l Na, 3 = 300 me/l Na. Shoot = S, root = R, WC = water content, Wt = weight.

Treatment	#S	S Height (cm)	SWC (%)	S Fresh Wt (gm)	Dry Wt (gm)		Succulence (F Wt/D Wt)
					S	R	
A1	25 ± 8	22 ± 2	291 ± 6	4.21 ± 1.45	1.08 ± 0.37	0.55 ± 0.09	3.91 ± 0.06
B1	27 ± 4	24 ± 1	295 ± 8	3.71 ± 0.55	0.94 ± 0.14	0.54 ± 0.06	3.95 ± 0.08
A2	20 ± 6	19 ± 3	266 ± 9	2.70 ± 0.88	0.73 ± 0.24	0.45 ± 0.09	3.66 ± 0.09
B2	15 ± 4	18 ± 1	265 ± 22	2.09 ± 0.75	0.55 ± 0.18	0.50 ± 0.06	3.65 ± 0.22
A3	17 ± 1	18 ± 1	262 ± 4	1.90 ± 0.16	0.53 ± 0.05	0.40 ± 0.02	3.62 ± 0.04
B3	-	-	-	-	0.35 ± 0.02	-	-
C	23 ± 7	21 ± 1	284 ± 7	3.20 ± 1.03	0.83 ± 0.27	0.42 ± 0.08	3.84 ± 0.07

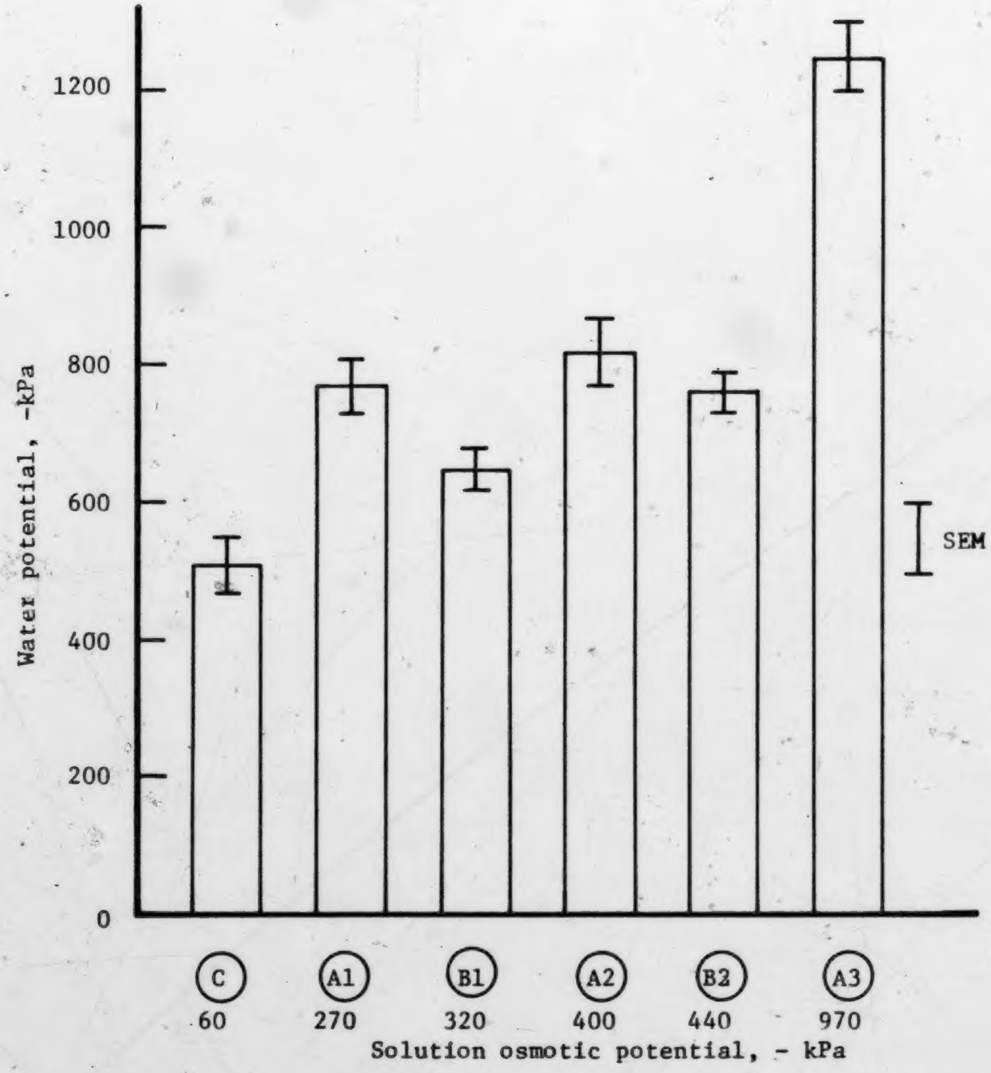

Figure 33. Mean water potential of saltgrass shoots grown at various Mg/Ca ratios and salt concentrations (Experiment 2). C = control (no added sodium), A = Mg/Ca = 5/1, B = Mg/Ca = 1/1, 1 = 50me/l Na, 2 = 100me/l Na, 3 = 300me/l Na.

potential was that of treatment A3 (-1252 kPa), which differed significantly from every other group. There were no significant differences between groups in the middle of the water potential range. There was a significant positive correlation (r = 0.858, $p<0.01$) between water potential of saltgrass shoots and osmotic potential of the solutions in which they were growing.

4.4.2.3 Tissue analyses

The raw data and statistical analyses of tissue cation concentrations and ratios are presented in Appendices 10 and 11. Treatment B3 tissue data in the following figures are shown as shoot data only, due to the lack of roots.

There were several notable effects of solution cation levels on tissue cation levels. The two calcium concentrations used in the A (low Ca) and B (high Ca) solutions resulted in considerable differences in tissue calcium concentrations (Figure 34). Group A plants had significantly lower calcium levels in shoot tissue than group B plants. This probably also applied to root calcium levels, but it was not possible to determine this. When the treatments were analyzed independently, there were no significant differences in shoot calcium concentrations between treatments. With respect to root calcium, treatment B2 was significantly higher than A1 and A2. Although the solution calcium concentration in treatment C was low like that in group A, the tissue levels were high like those in

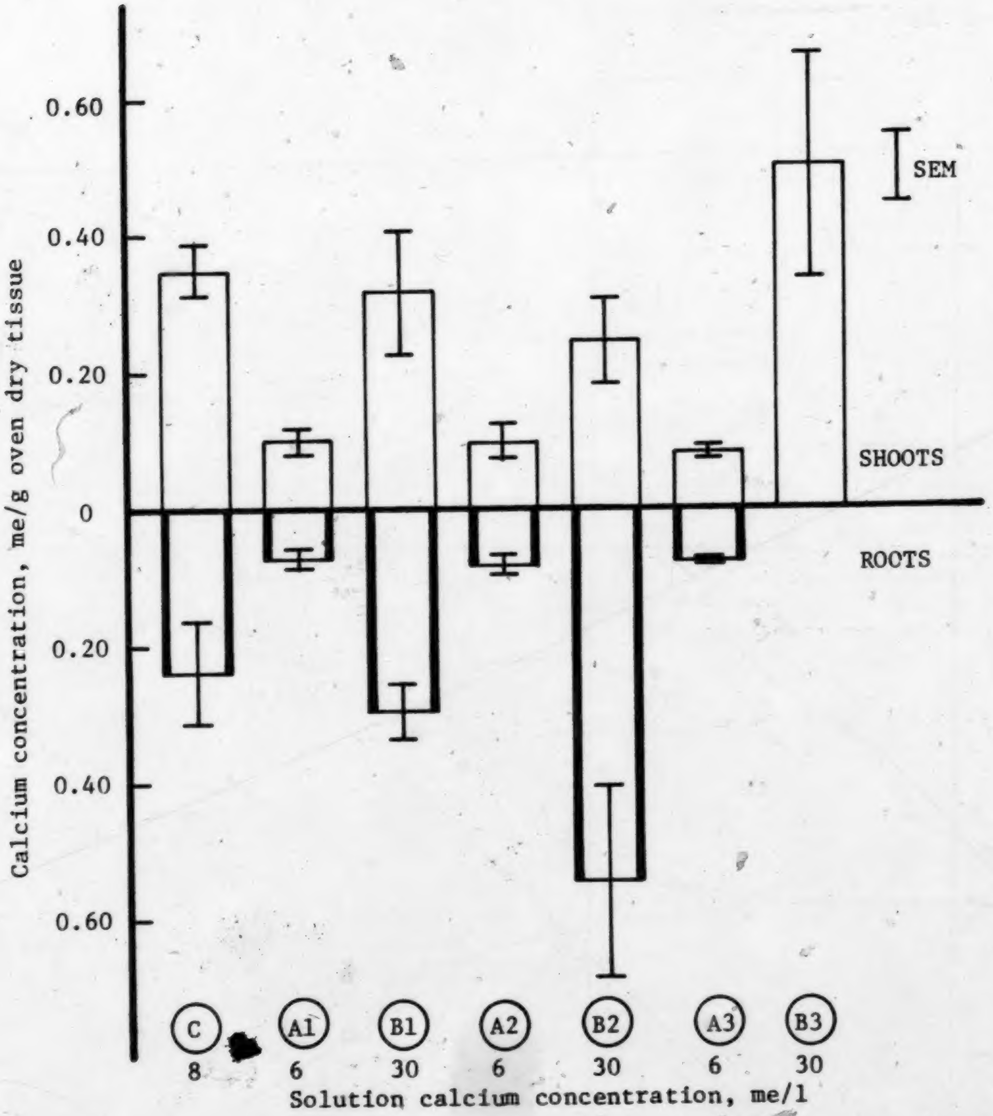

Figure 34. Mean calcium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2). See Figure 33 for explanation.

group B.

There was not a great deal of variation in shoot magnesium concentrations among the seven treatments (Figure 35), and there were no significant differences found. With respect to root magnesium concentration, the low value of the control was significantly different from all other treatments.

The widest range of values was found in sodium concentration (Figure 36). The mean sodium concentration in shoot tissue ranged from 0.05 me/g in C (which had no sodium added to the solution) to 0.78 me/g in B3 (300 me/1 added Na), and in root tissue from 0.04 me/g in C to 0.57 me/g in A3 (300 me/1 added Na). There were significant differences in shoot sodium content between groups 1 (50 me/1 of solution Na) and 3 (300 me/1) and between groups 2 (100 me/1 of Na) and 3. The very high shoot sodium concentration in treatment B3 was significantly different from that in treatments A1, B1, B2 and C. In root tissue, both the low sodium concentration in treatment C and the high one in A3 differed significantly from all other treatments.

The extremely low potassium concentration in tissue from treatment B3 (Figure 37) seems to have biased the two-way ANOV of shoot tissue, making the results inconclusive. The analysis shows that groups A and B differed significantly with respect to shoot potassium concentration, but the differences were not consistent. The extreme difference between B3 and all other groups was

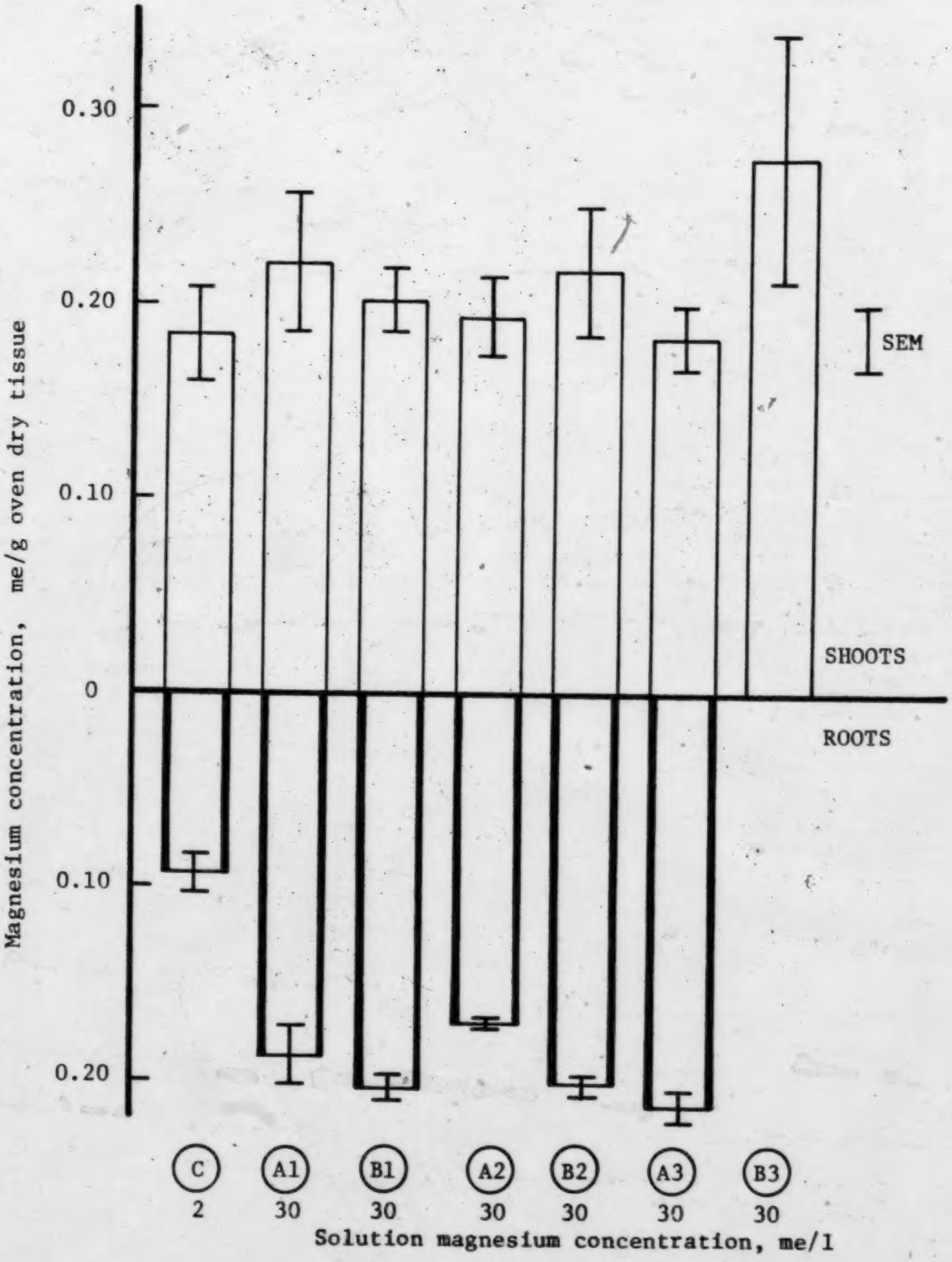

Figure 35. Mean magnesium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2). See Figure 33 for explanation.

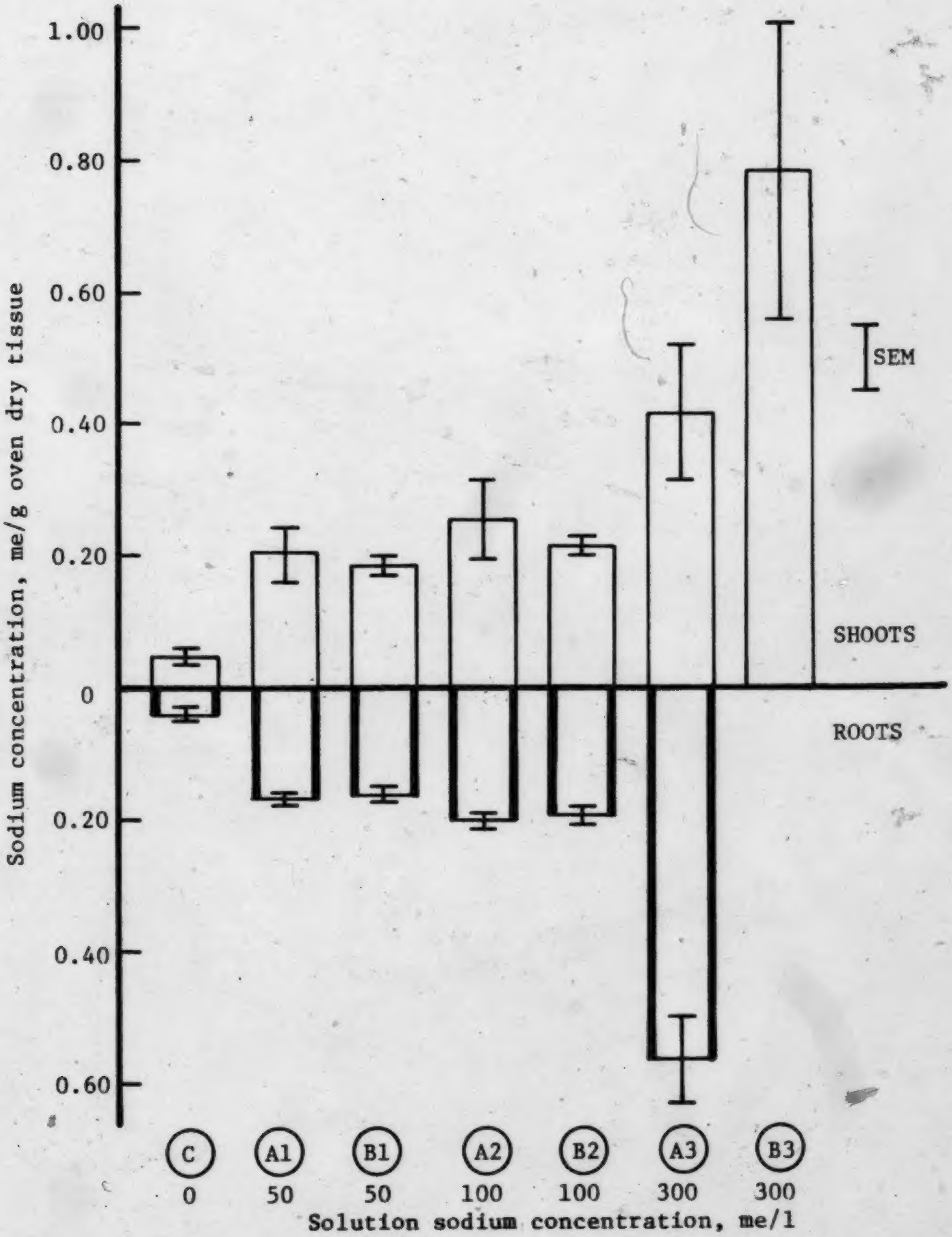

Figure 36. Mean sodium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2). See Figure 33 for explanation.

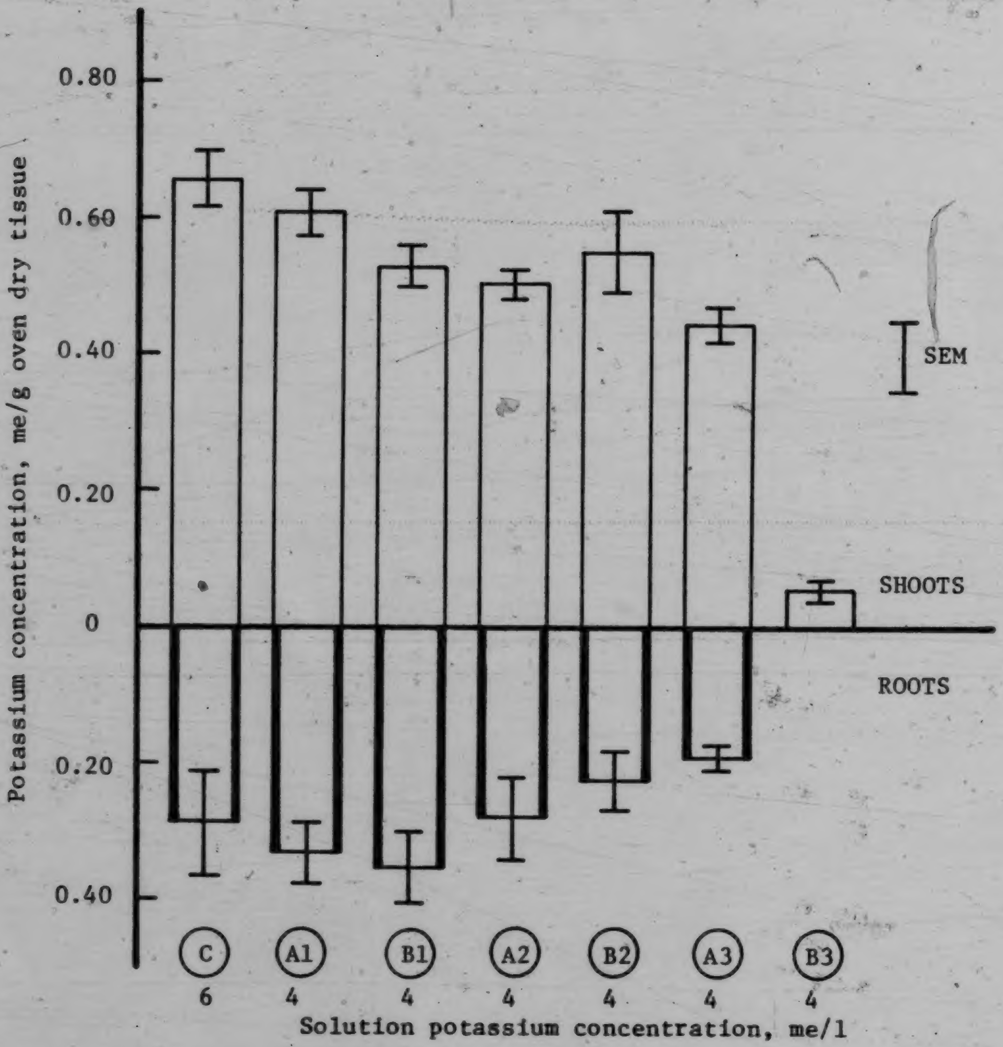

Figure 37. Mean potassium concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2). See Figure 33 for explanation.

apparently large enough to cause the significant differences between groups A and B, 1 and 3, and 2 and 3. The one-way ANOV showed significant differences in shoot K concentration between B3 and all other treatments. Although the root potassium contents (which were much lower than shoot contents) tended to decrease somewhat as solution sodium concentration increased, there were no significant differences between treatments.

Total cation concentrations in tissue are shown in Figure 38. Although the B group had slightly higher shoot concentrations than the A group, there were no significant differences found. Root total cation levels, which were not as high as those for shoots, tended to increase somewhat as solution total cation concentrations increased. The highest root total cation concentration, in B2, was significantly different from A1, A2 and C. Treatment C, which had the lowest concentration, also differed significantly from treatment B1.

The use of three solution Mg/Ca ratios led to large differences in tissue Mg/Ca ratios of the seven treatments (Figure 39). The high shoot ratios in group A were significantly different from the low shoot ratios in group B. The one-way ANOV showed that each A treatment differed significantly from C, B1, and B3. The differences in Mg/Ca ratios in the roots were even more pronounced. Each of treatments A1, A2 and A3 (which had high Mg/Ca ratios) differed significantly from treatments C, B1 and B2 (which

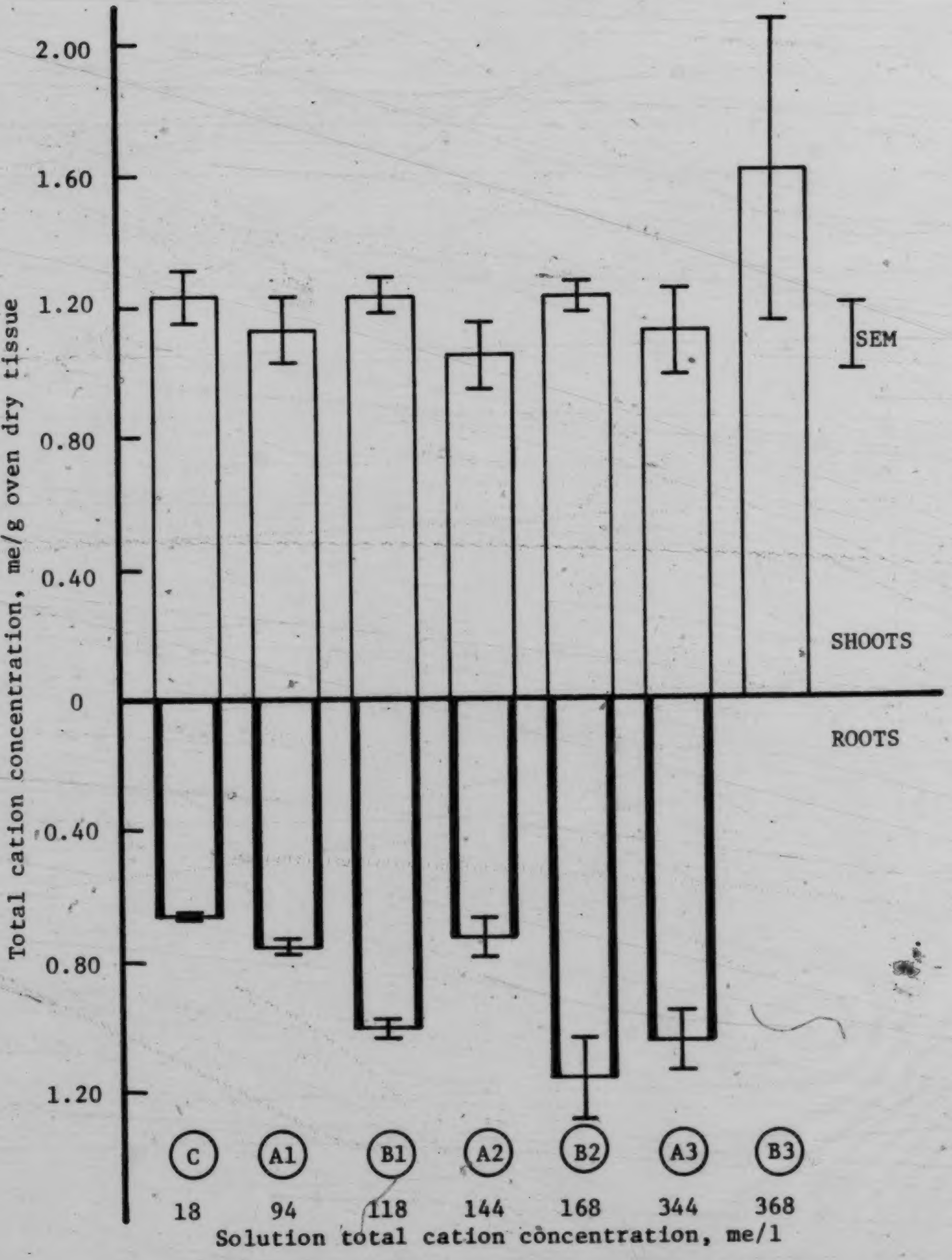

Figure 38. Mean total cation concentration in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2). See Figure 33 for explanation.

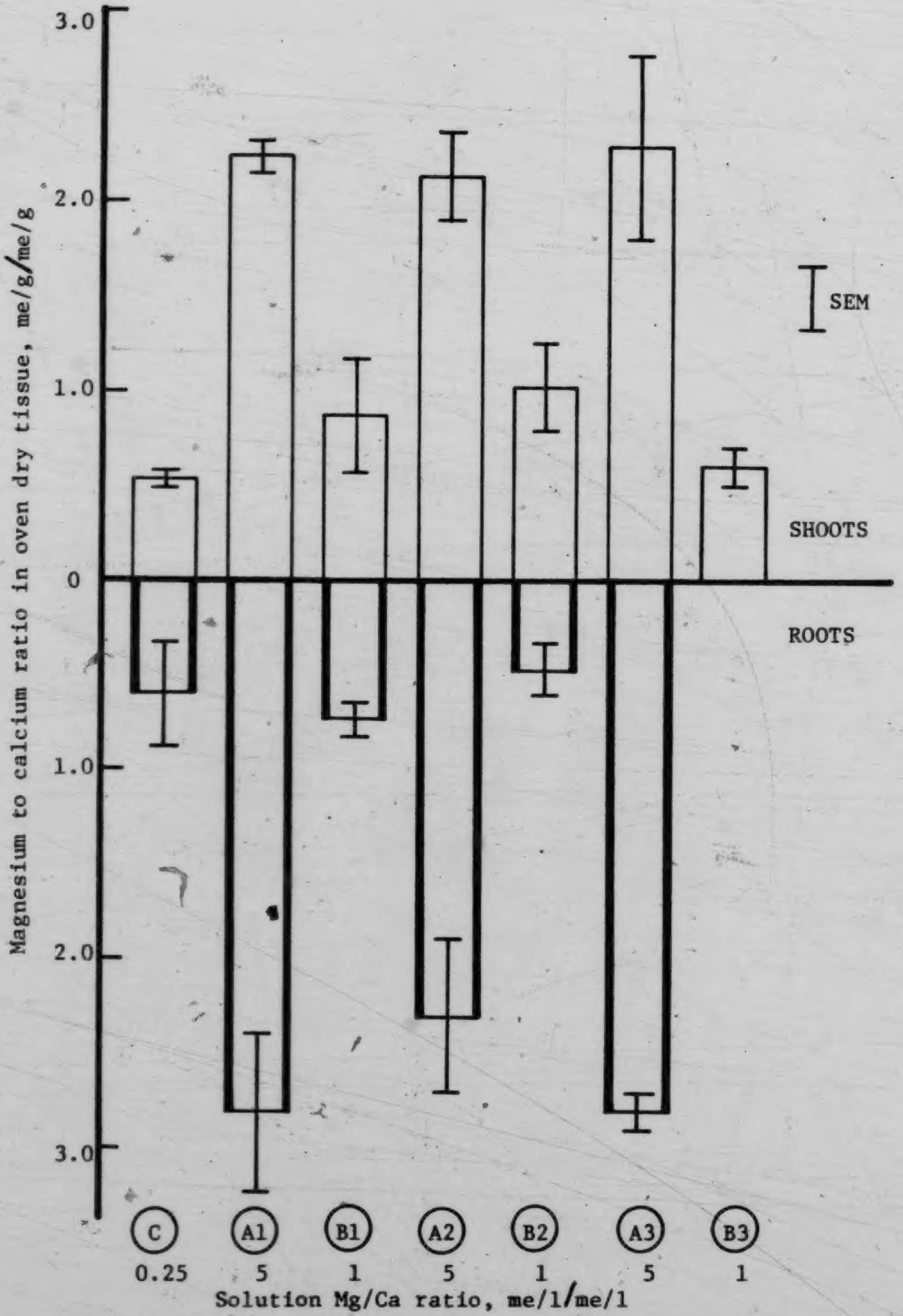

Figure 39. Mean Mg/Ca ratios in saltgrass grown at various Mg/Ca ratios and salt concentrations (Experiment 2). See Figure 33 for explanation.

had much lower ratios).

The proportions of the four major cations in the treatment solutions are shown in Figure 40. Upon comparing these to Figure 41, which shows the proportions of the cations in saltgrass tissue, one can see that the plants did not absorb all the cations in amounts directly related to their proportions in solution. As in solution culture Experiment 1, the plants were selectively absorbing potassium more than the other cations. Treatment B3, in which all plants died by the halfway point of the experiment, had the lowest tissue K/TC ratio and differed significantly from all other treatments.

Although there was no sodium added to the control solution, sodium accounted for 4 to 6% of the total cations in shoot and root tissue of treatment C. In the other treatments, the proportion of sodium ranged from 15 (B1) to 50% (B3) of total shoot cations and from 16 (B1) to 54% (A3) in the roots. These wide ranges accounted for many significant differences in Na/TC between groups and treatments (Appendix 11). Group 3 (high solution Na/TC) differed significantly from groups 1 and 2 (lower solution Na/TC) with respect to shoot Na/TC. In most cases treatments with the highest (A3, B3) or lowest (C) values differed significantly from all others.

There was not much variation in shoot Mg/TC ratios among the treatments, and there were no significant differences found. The lowest root Mg/TC ratio was found in

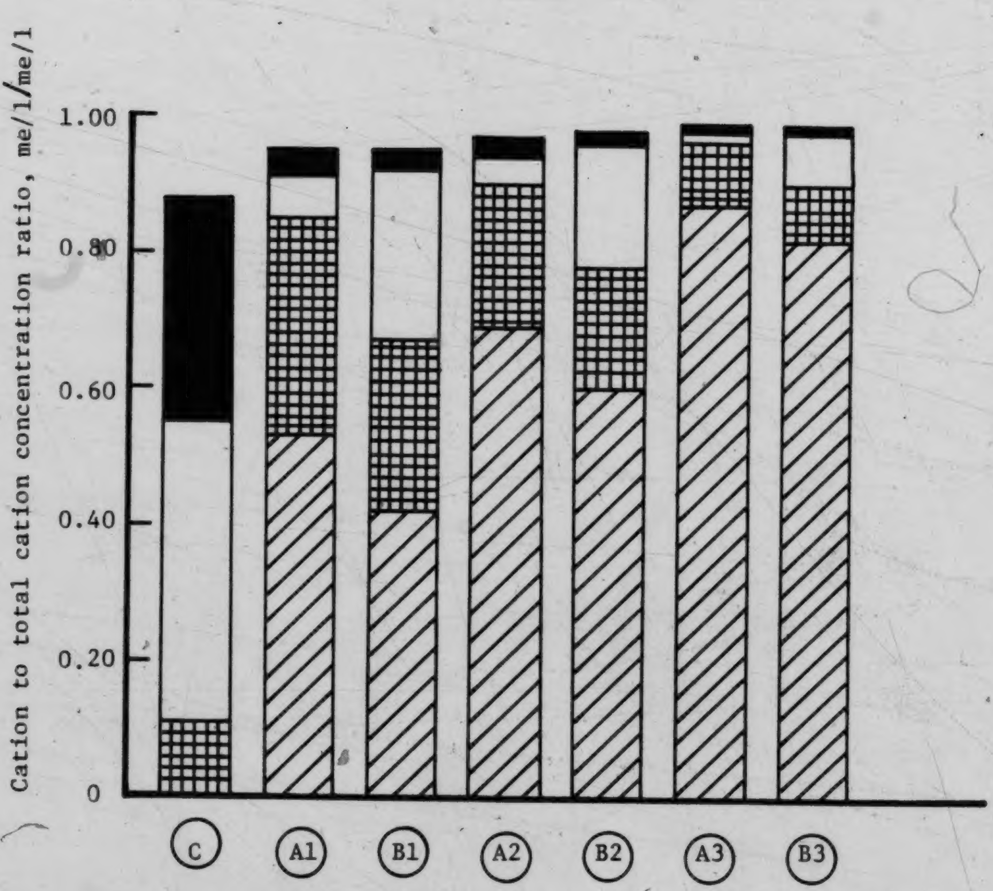

Figure 40. Cation to total cation concentration ratios in solutions C to B3 of Experiment 2. The NH_4/TC ratio brings the total for each solution to 1.00. Na/TC ▨ , Mg/TC ▦, Ca/TC ☐, K/TC ■ . C = control (no added sodium), A = Mg/Ca = 5/1, B = Mg/Ca = 1/1, 1 = 50me/1 Na, 2 = 100me/1 Na, 3 = 300me/1 Na.

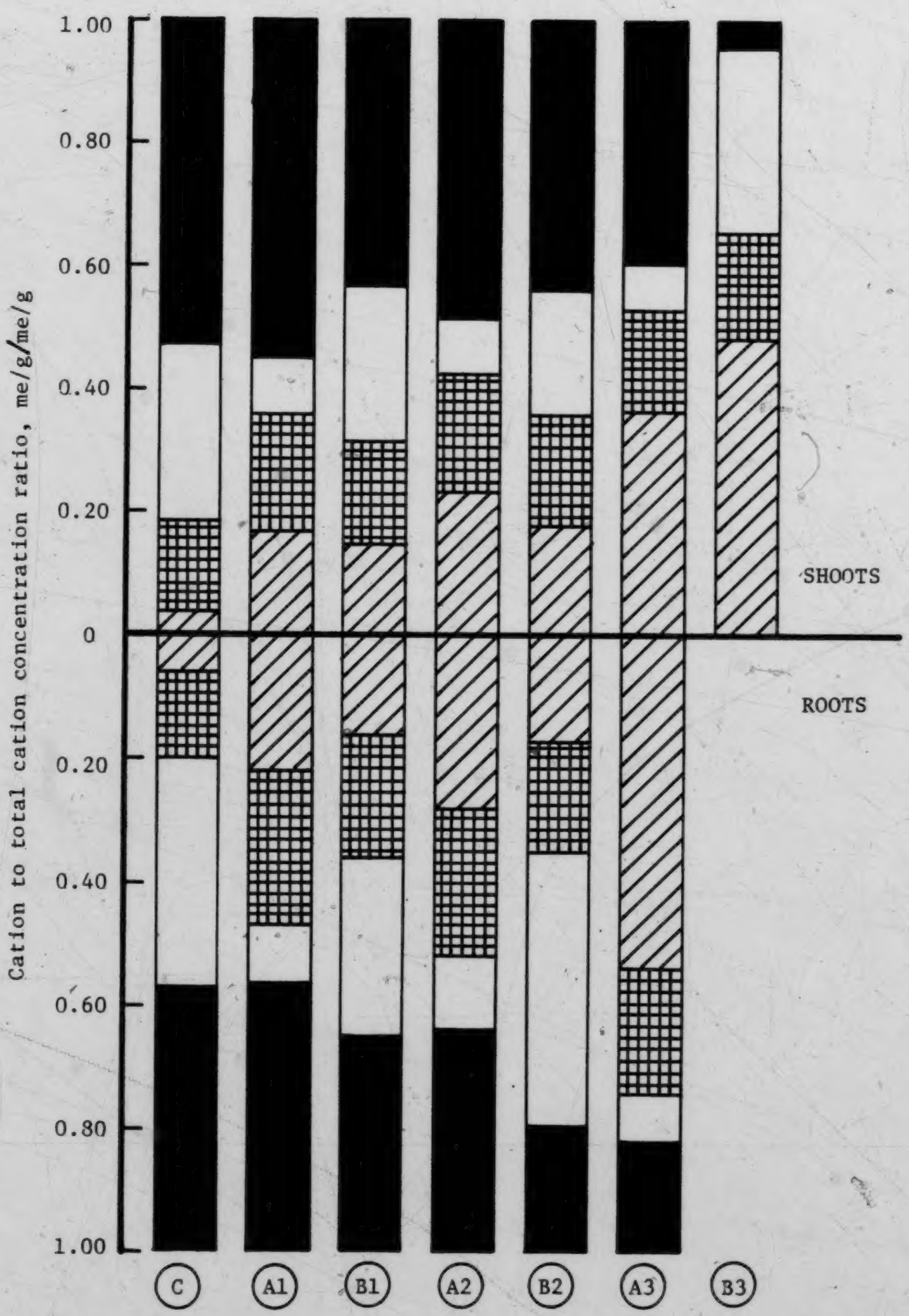

Figure 41. Cation to total cation concentration ratios in saltgrass grown at various Mg/Ca ratios and salt concentrations. See Figure 40 for legend.

treatment C, which significantly differed from A1 and A2.

There was considerable variation in Ca/TC ratios among the treatments. Group A (low solution Ca/TC) had low Ca/TC ratios in the shoot tissue, and was significantly different from group B (high solution Ca/TC). The high shoot Ca/TC ratio of treatment C differed significantly from those in A1 and A2, while the higher value in B3 was significantly different from those in A1, A2 and A3. There was a considerable amount of between treatment variation in root Ca/TC, but due to the large amount of within treatment variation, there were no significant differences.

Significant correlations were found between dry weight of saltgrass shoots, and magnesium, sodium and potassium shoot concentrations, as well as shoot Mg/TC, Na/TC and K/TC ratios (Appendix 12). Root dry weight was significantly correlated with root potassium concentration and the K/TC ratio in the roots.

The results of the barley tissue analyses are presented in Appendix 8. The tissue calcium concentrations reflected solution calcium concentrations, with the B group having higher calcium content than the A group. The calcium concentration in the barley control was considerably higher than that in the corresponding saltgrass treatment. There was little difference in magnesium concentration among A and B barley treatments. The control treatment again had somewhat higher magnesium concentrations than the saltgrass control. Sodium concentrations in the A and B barley treatments were many times greater than those found in saltgrass tissue, but the barley control had sodium levels comparable to those of the saltgrass control. The A and B group barley treatments had tissue potassium concentrations which were generally lower than those found in saltgrass tissue, but the control barley treatment potassium concentrations were higher than those found in any saltgrass treatment. All of the total cation concentations in the seven barley treatments were higher than those in the corresponding saltgrass treatments.

The Mg/Ca ratio in barley treatments followed no consistent pattern. The shoot and root Mg/Ca ratios of the barley control were similar to those in the saltgrass control. The cation proportions in the A and B barley treatments were quite different from those in the corresponding saltgrass treatments. Sodium ranged from 46 to 72% of total shoot cations and from 30 to 66% of total root cations. The proportion of magnesium in shoots and roots ranged from about 10 to 30%, while calcium varied from about 10 to 70% depending on treatment. Root calcium proportions reflected the difference in calcium content of the A and B solutions. K/TC ratios were very low in the A and B barley treatments. They ranged from 2 to 14% in shoot and root tissue, which was not nearly as high as the 20 to 55% found in saltgrass shoot and root tissue grown under the same conditions. The cation to total cation ratios in the barley control, including the K/TC ratio, were similar to those of the corresponding saltgrass treatment.

The results of Experiment 2 indicate that shoot water potentials and cation concentrations and ratios of saltgrass tissue were significantly affected by the range of sodium concentrations and Mg/Ca ratios used in the growth solutions. However, as in Experiment 1, internal changes were not accompanied by significant external changes in the plants. Barley grown in the solutions with added sodium sulfate did not survive, but control barley plants thrived.

4.5 Germination

4.5.1 Germination of seeds in osmotica

The results of the germination experiment are shown in Figure 42, and statistical analyses are presented in Appendix 13. Decreasing solution osmotic potentials delayed germination as compared to control treatments. Maximum germination percentages were reached between three and six days for essentially all of the distilled water and -200 kPa replicates, and between six and nine days for the -500 and -1000 kPa replicates. No germination had occurred in any of the -2000 kPa treatments by the fourteenth day.

Germination was highest in solutions of the two sodium salts, and lowest in solutions of PEG. There were significant differences between the entire sodium chloride group and both the magnesium sulfate and the PEG groups. There were no significant differences in germination between salt treatments at 0, -200 and -2000 kPa. At -500 kPa, the

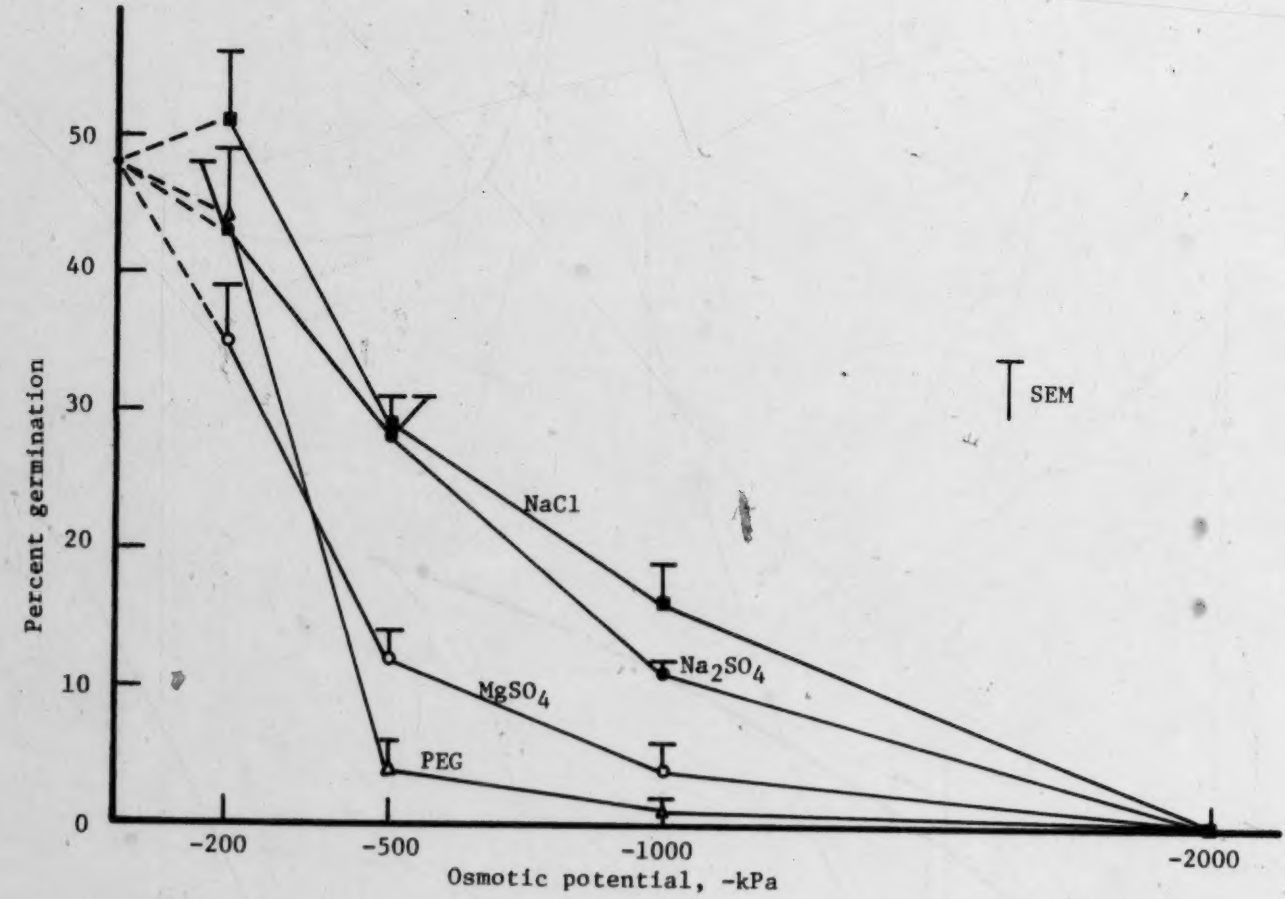

Figure 42. Mean percent germination of saltgrass seeds placed in four osmotica. Distilled water was used for the germination treatment at 0 kPa.

two sodium salts were significantly different from both magnesium sulfate and PEG. At -1000 kPa germination in both sodium salts significantly differed from that in PEG, but only the NaCl treatment was significantly different from the magnesium sulfate treatment.

Decreasing osmotic potentials resulted in decreased germination percentages for all four osmotica. All water potential groups were significantly different from one another except 0 and -200 kPa, and -1000 and -2000 kPa. For all four osmotica, the -200 kPa treatment was significantly different from the -1000 and -2000 kPa treatments. For magnesium sulfate, sodium chloride and PEG, the -200 and -500 kPa treatments were also significantly different. For both sodium salts, the -500 and -2000 kPa treatments were significantly different, while the -500 and -1000 kPa treatments differed significantly for only sodium sulfate.

The germination results show that decreasing water potential was not the only factor determining the magnitude of germination; the type of salt was also important. There was also significant interaction between the two factors.

4.5.2 Recovery of germination ability

The results of germination recovery are presented in Table 13. Recovery was poor in many treatments due to mold formation on the seeds. In no treatment did recovery increase the total percentage of germination to equal that in distilled water. It is felt that the presence of mold

Table 13. Recovery of germination ability by osmotically stressed saltgrass seeds. Values given are means (plus or minus SEM) of five replicates.

Osmotic potential (kPa)	Total % germination in osmoticum	Total % germination after recovery period
distilled H_2O		
0	48 ± 3	
Na_2SO_4		
-200	43 ± 5	46 ± 5
-500	28 ± 3	30 ± 3
-1000	11 ± 1	19 ± 3
-2000	0 ± 0	14 ± 2
$MgSO_4$		
-200	35 ± 4	36 ± 4
-500	12 ± 2	14 ± 2
-1000	4 ± 2	11 ± 2
-2000	0 ± 0	9 ± 4
NaCl		
-200	51 ± 5	51 ± 5
-500	29 ± 2	32 ± 2
-1000	16 ± 3	22 ± 2
-2000	0 ± 0	14 ± 5
PEG		
-200	44 ± 5	46 ± 4
-500	4 ± 2	12 ± 3
-1000	1 ± 1	1 ± 1
-2000	0 ± 0	25 ± 9

greatly decreased the number of germinable seeds, making the results inconclusive.

5. DISCUSSION

5.1 The Physical Environment

5.1.1 Micrometeorological data

The temperature, humidity and precipitation data indicate that the *Distichlis stricta* community at Akasu Lake experienced climatic conditions in 1978 which were typical for that area. The warm daytime temperatures, fairly high relative humidity, and adequate precipitation in late spring and early summer provided favorable conditions for rapid growth of plants.

5.1.2 Soil physical measurements

The combination of increased air temperatures and decreased precipitation promoted increased soil temperatures and a drop in soil moisture levels from late June to early August. This coincided with growth cessation by both tall and short saltgrass plants.

Soil temperatures were higher and moisture levels lower in the short Ds zone than in the tall Ds zone, suggesting that these factors affect growth limitation.

Since both the field moisture levels and the moisture capacity at saturation were lower for short Ds than tall Ds soils, the ratio of saturation percent to Pw was similar for both soils. This indicates that if salt concentrations in the saturation extracts were similar for both soils, the salt concentrations in the field soil solutions would also be similar.

Field soil moisture percentages (Pw) and saturation percentages (SP) from several areas in North America are shown in Table 14. These values are from soils on which *Distichlis stricta* was growing as a dominant or an associated species. Soil moisture ranges from 4% for the *Sporobolus-Distichlis* community in Oklahoma to 61% for the *Distichlis* community in North Dakota. Field moisture and saturation percentages for the tall saltgrass communities tended to be higher than those for the dwarf (short) saltgrass communities in the areas sampled. Although comparison of these measurements is limited by differences in environmental conditions at sampling time, it appears that low soil moisture contributes to the depressed growth of dwarf saltgrass.

5.1.3 Soil chemical analyses

Comparisons of soil chemical data from the short, tall and tall, scattered (*Distichlis-Hordeum*) Ds zones of this study with data from other areas are presented in Tables 14, 15 and 16. Soil pH ranges from 7.1 in the *Suaeda-Chenopodium* community in southern Alberta to 8.8 in the dwarf saltgrass community in Kansas, with most pH values falling between 7.5 and 8. Although soil pH may differ under different stands of saltgrass, it tends to remain fairly constant in each soil over the growing season, as shown by this study and by Hansen et al. (1976).

Table 14. Physical and chemical characteristics of surface soils under saltgrass stands. Pw = soil moisture percent. SP = saturation percent. ECe = electrical conductivity in mS/cm at 25 C.

Location and Reference	Pw	SP	pH	ECe	Community Dominants
Nonsaline soils, U.S. (Richards 1954)	-	32-40	6.4-7.9	0.6-1.7	
Alberta (Keith 1958)	-	-	8.2	28-53	*Distichlis*
	-	-	7.2	8-15	*Hordeum*
	-	-	7.1	38	*Suaeda*-*Chenopodium*
Saskatchewan (Dodd et al. 1964)	-	-	8.3	23	*Puccinellia*-*Distichlis*
	-	-	7.9	15	*Distichlis*-*Agropyron*
	-	-	8.2	19	*Distichlis*
North Dakota (Hadley and Buccos 1967)	-	-	-	11-12	*Distichlis*-*Hordeum*-*Poa*
	-	-	-	17-23	*Distichlis*-*Hordeum*
	-	-	-	27-28	*Salicornia*-*Suaeda*
North Dakota (Redmann 1972)	45-58	-	7.5	16	*Hordeum*
	49-61	-	7.4	21	*Distichlis*
South Dakota (Ungar 1970)	25	38	8.3	19	Dwarf *Distichlis*
	40	59	7.9	7	*Distichlis*-*Hordeum*
	34	64	7.7	7	*Distichlis*-*Agropyron*
Nebraska (Ungar et al. 1969)	25	59	7.7	67	Dwarf *Distichlis*
	34	71	7.9	9	Tall *Distichlis*
	36	71	7.7	2	*Distichlis*-prairie
Colorado (Ungar 1974a)	14	-	7.7	46	Dwarf *Distichlis*
Kansas (Ungar 1965)	-	59	8.1	-	Tall *Distichlis*
	-	47	8.5	-	*Scirpus*-*Distichlis*
	-	51	8.1	-	*Distichlis*-*Suaeda*
	-	56	8.3	-	*Spartina*-*Distichlis*
Kansas (Ungar 1967)	22	52	8.8	73	Dwarf *Distichlis*
	46	78	7.6	14	Tall *Distichlis*
	41	68	7.3	11	*Hordeum*-*Iva*-*Distichlis*
Oklahoma (Ungar 1968)	25	59	8.2	42	Dwarf *Distichlis*
	22	58	8.2	6	*Distichlis*-*Hordeum*
	4	26	8.7	2	*Sporobolus*-*Distichlis*
Alberta (L'Hirondelle)	29	50	8.3	33	Dwarf *Distichlis*
	39	64	8.3	35	Tall *Distichlis*
	29	60	8.0	8	*Distichlis*-*Hordeum*

Table 15. Cation concentrations (in me/l) and percent salts of surface soils under saltgrass stands. TC = total cation concentration.

Location and Reference	Ca	Mg	Na	K	TC	% Salts	Community Dominants
Nonsaline soils, U.S. (Richards 1954)	2.7-3.3	1.7-2.3	1-12	0.2-0.9	7-18		
Alberta (Keith 1958)	-	-	-	-	-	1.0-2.4	*Distichlis*
	-	-	-	-	-	0.3-0.5	*Hordeum*
	-	-	-	-	-	1.5	*Suaeda*-*Chenopodium*
Saskatchewan (Dodd et al. 1964)	20	425	237	3.9	686	-	*Puccinellia*-*Distichlis*
	24	44	142	1.6	211	-	*Distichlis*-*Agropyron*
	19	131	138	3.1	291	-	*Distichlis*
South Dakota (Ungar 1970)	-	-	-	-	-	2.8	Dwarf *Distichlis*
	-	-	-	-	-	1.1	*Distichlis*-*Hordeum*
	-	-	-	-	-	1.1	*Distichlis*-*Agropyron*
Nebraska (Ungar et al. 1969)	-	-	-	-	-	4.2	Dwarf *Distichlis*
	-	-	-	-	-	0.6	Tall *Distichlis*
	-	-	-	-	-	0.1	*Distichlis*-prairie
Colorado (Ungar 1974a)	-	-	-	-	-	3.6	Dwarf *Distichlis*
Kansas (Ungar 1965)	-	-	-	-	-	0.3-0.9	Tall *Distichlis*
	-	-	-	-	-	0.3-1.1	*Scirpus*-*Distichlis*
	-	-	-	-	-	0.5-2.5	*Distichlis*-*Suaeda*
	-	-	-	-	-	0.2-1.0	*Spartina*-*Distichlis*
Kansas (Ungar 1967)	-	-	-	-	-	2.4	Dwarf *Distichlis*
	-	-	-	-	-	0.7	Tall *Distichlis*
	-	-	-	-	-	0.5	*Hordeum*-*Iva*-*Distichlis*
Oklahoma (Ungar 1968)	-	-	-	-	-	1.3	Dwarf *Distichlis*
	-	-	-	-	-	0.2	*Distichlis*-*Hordeum*
	-	-	-	-	-	0.04	*Sporobolus*-*Distichlis*
Alberta (L'Hirondelle)	24	104	261	2.9	390	1.3	Dwarf *Distichlis*
	26	134	263	2.3	425	1.3	Tall *Distichlis*
	9	17	47	0.7	75	0.4	*Distichlis*-*Hordeum*

Table 16. Cation ratios (me/l to me/l) of surface soils under saltgrass stands. TC = total cation concentration, SAR = sodium adsorption ratio.

Location and Reference	Mg/Ca	Na/TC	Mg/TC	Ca/TC	K/TC	SAR	Community Dominants
Nonsaline soils, U.S. (Richards 1954)	0.58-0.83	0.17-0.67	0.11-0.32	0.18-0.38	0.02-0.12	1-8	
Saskatchewan (Dodd et al. 1964)	22	0.35	0.62	0.03	0.006	16	*Puccinellia*-*Distichlis*
	2	0.67	0.21	0.11	0.007	24	*Distichlis*-*Agropyron*
	7	0.47	0.45	0.06	0.011	16	*Distichlis*
Alberta (L'Hirondelle)	4	0.65	0.27	0.06	0.007	34	Dwarf *Distichlis*
	5	0.60	0.33	0.07	0.006	28	Tall *Distichlis*
	2	0.64	0.22	0.13	0.010	14	*Distichlis*-*Hordeum*

There is a large range of ECe values of soils in which saltgrass is established. Ungar (1968) reported an ECe of 1.9 mS/cm (which is almost as low as that of a nonsaline soil) for the *Sporobolus-Distichlis* community in Oklahoma, while values from 56 to 104 (mean 73) have been reported for dwarf saltgrass soils in Kansas (Ungar 1967). In general the ECe values and salt percentages for the dwarf saltgrass communities tend to be considerably higher than those for the tall saltgrass communities, although this is not always the case. In this study, the ECe of soil under tall saltgrass averaged somewhat higher than that for the short form. Soil from both short and tall zones had much higher values than soil under the tall, scattered zone.

There are few data available concerning cation relations in soil solutions of halophyte communities. Dodd et al. (1964) analyzed soil saturation extracts for several halophyte communities in Saskatchewan. Akasu Lake soil data for the three Ds zones are similar to those for the *Puccinellia-Distichlis*, *Distichlis-Agropyron*, and *Distichlis* communities described by Dodd et al., with the exception of magnesium concentrations and ratios. The high magnesium concentrations in two of the Saskatchewan soils resulted in higher Mg/Ca and Mg/TC ratios and higher total cation concentrations than found in the Akasu Lake soils. However, the Ca, Na and K concentrations were similar (Table 16). The Ca/TC ratios in the Saskatchewan and Alberta soils (Table 16) were lower than the 0.15 to 0.20 considered necessary for optimum crop growth, and the K/TC ratios were much lower than those usually found in nonsaline soils. At Akasu Lake, the tall, scattered growth form associated with *Hordeum* was growing on soils with consistently higher Ca/TC and K/TC, and lower Mg/TC than the dwarf and tall forms.

The high SAR present in saltgrass soils indicates that sodium is dominant over the divalent cations, and that uptake of cations other than sodium will be more difficult than in nonsaline soils. High SAR in the saline soils described does not reflect poor soil structure, because very high salt concentrations keep soil particles flocculated.

It would be interesting to see how cation ratios vary in soils of halophyte communities across North America. It is possible that the nutrients present in low proportions have as much influence on halophyte distribution and growth form as total salt concentration, since ion uptake strategies can be very different in different halophyte species.

Calculation of soil osmotic potential using the formula described by Richards (1954) revealed that the short and tall Ds zone soils had OPs of -2000 kPa, while the tall, scattered Ds zone soil had an OP of only -800 kPa. Since ECe, % salt and OP are all closely related, they show the same trends: the dwarf growth form of saltgrass is almost always found growing in soils with high ECe, high % salt and low OP, while the tall form usually is found with other species where soil ECe and % salt are lower and OP is higher. Soils under the tall saltgrass form described by other authors are comparable to those under the tall, scattered form described for Akasu Lake, while the Akasu Lake short form soils correspond to the dwarf form soils of other authors. Soils under the tall dominant form described in this study are chemically most like those of the dwarf growth form.

From the information available on soils of halophyte communities, the following conclusions may be drawn. Where soil physical characteristics are relatively constant, increases in total salinity appear to be limiting to plant growth. Where soil chemical characteristics are relatively constant, low soil moisture and/or high soil temperatures become important limiting factors.

The conductivity of Akasu Lake water samples showed that the water was moderately saline. This water, which was the source of the salts present in the soils under the *Distichlis stricta* community, had somewhat more extreme cation ratios than those in the soil solution. The Na/TC and K/TC ratios were higher and the Mg/TC and Ca/TC ratios were lower than those in the soil solutions.

Rawson and Moore (1944) analyzed water samples from 53 saline lakes in Saskatchewan. The Akasu Lake water data fall well within the reported ranges for these lakes. They found calcium concentrations from 0.4 to 26 me/l, with a median of 2.5 me/l. The Akasu Lake calcium range was 1.1 to 1.9 me/l. Magnesium ranged from very low (0.7 me/l) to very high (930 me/l) with a median of 8.3 me/l in the Saskatchewan lakes. The Akasu Lake magnesium concentration was from 4.5 to 5.0 me/l. Potassium varied from 0.09 to 26 me/l, with a median of 0.57 me/l in the Saskatchewan lakes, while in Akasu Lake it ranged from 0.7 to 1.3 me/l. Sodium concentration in the Saskatchewan lakes had a range of 0.06 to 780 me/l, with a median of 4.3 me/l. In Akasu Lake water it ranged from 32 to 37 me/l. The cation concentration ranges reported for saline springs in Utah (Bolen 1964) are also similar to those of Akasu Lake. The ranges for the Utah waters were Ca 4.1 to 6.3 me/l, Mg 3.7 to 4.4 me/l, Na 21 to 32 me/l, and K 1.1 to 1.3 me/l.

The reliability of ECe in predicting total cation concentration was reported by Richards (1954). Data from the Akasu Lake soil and water samples also showed a strong correlation between EC and TC. For rapid soil characterization, ECe is useful in assessing the degree of total salinity in various halophyte communities.

5.2 Community Characterization

5.2.1 Description of species present

Most of the species present in the vicinity of the *Distichlis stricta* community at Akasu Lake are typically found in saline areas in Alberta (Moss 1959), and many are common to halophyte communities in several areas of North America (Ungar 1974b). Three species--*Hordeum jubatum*, *Puccinellia nuttalliana* and *Suaeda calceoliformis*--which are most consistently associated with *D. stricta* in other areas, were also found with saltgrass at Akasu Lake. The shore to shore transect showed that the species present were distributed as expected based on reports from many other areas. *Suaeda* and *Distichlis* grew on soils with the highest salinites, while *Puccinellia* and *Hordeum* were present on soils with somewhat lower salinities. The composites were found on soils with even lower salinities, while the Cyperaceous species were prevalent on soils with very high moisture contents (i.e. closer to shore).

5.2.2 Community sampling

The generally low cover values and low species diversity found in this study are typical of many halophyte communities in which saltgrass grows. Ungar (1965) reported basal area values from 1.2% in the *Distichlis-Suaeda* community to 12.3% in the tall *Distichlis* meadow community at the Big Salt Marsh in Kansas. The latter community also had the greatest species diversity; there were 13 species present, although only five contributed noticeably to the cover value. Saltgrass had the highest or second highest cover value in most of the communities in which it occurred.

At Akasu Lake *Distichlis*, *Hordeum* and *Puccinellia* had the highest cover values in nearly all of the quadrats sampled, depending on proximity to shore. In other areas, including Saskatchewan, Kansas, Oklahoma, Nebraska, North Dakota, South Dakota and Colorado, saltgrass also had high relative percent cover in the communities in which it was dominant or codominant, although total percent cover was often very low (Dodd and Coupland 1966b, Ungar 1967, 1968, 1970, 1974a, Ungar et al. 1969, Redmann 1972).

In almost every community in which it occurs in North America, *Distichlis stricta* has very high frequencies, usually close to 100% (Ungar 1965, 1967, 1968, 1970, 1974a, Ungar et al. 1969). Other species have low frequencies in the dwarf saltgrass communities, and low to high frequencies when associated with tall saltgrass. Species with the highest frequencies in saltgrass communities include *Suaeda calceoliformis* (Saskatchewan, Dodd and Coupland 1966b; Kansas, Ungar 1965), *Aster ericoides* (Saskatchewan, Dodd and Coupland 1966b), *Hordeum jubatum* (Oklahoma, Ungar 1968; South Dakota, Ungar 1970), and *Puccinellia nuttalliana* (Alberta, Keith 1958). In the two areas sampled at Akasu Lake, the highest frequencies were those of *Hordeum*, *Distichlis*, *Puccinellia*, *Suaeda*, *Chenopodium*, and *Aster brachyactis*. High frequency values did not necessarily indicate high cover values. A comparison of frequency and cover values for the two areas sampled showed that community composition could change considerably over a short distance. *Suaeda* and *Puccinellia* were more abundant in area 2, where they grew with the short form of saltgrass in more saline soils, than in area 1 where they grew with both short and tall saltgrass in less saline soils.

5.2.3 Saltgrass zone transects

The two transects through the saltgrass zone at Akasu Lake clearly showed the dominance of *Distichlis stricta* when it occurred as the short growth form. In the short Ds zone it formed a nearly monospecific stand with very high percent cover. The areas north and south of this stand had lower soil salinities and higher cover of species other than saltgrass. The tall, scattered Ds zone is actually a *Distichlis-Hordeum* or *Hordeum-Distichlis* zone, because the drop in percent cover due to saltgrass coincided with an increase in percent cover of *Hordeum*.

It must be emphasized again that the distinction between the short and the tall growth forms of saltgrass is somewhat arbitrary, because these forms are actually endpoints of a gradient of culm height. However, certain combinations of edaphic factors result in mean plant heights which tend to be near the relatively short or relatively tall end of the gradient.

It is interesting that saltgrass reached its highest percent cover when it was present as the short growth form rather than the tall growth form. The soils under the short and tall Ds zones both had high salinity, but soil moisture levels were consistently higher in the tall Ds zone. Soils of the tall *Distichlis-Hordeum* zone had much lower salinities than those of both the short and tall Ds zones. Apparently a combination of high soil salinity and relatively low soil moisture reduces or eliminates competition from other species, allowing dwarf saltgrass to spread out and dominate such areas. This type of species distribution has been found by other authors. Ungar et al. (1979) suggested that some form of interspecific competition limited *Salicornia europea* to soil zones with less than optimal conditions for its growth.

5.3 Growth of Saltgrass in the Field

5.3.1 Phenological observations

The growth patterns of *Distichlis stricta* were well correlated with seasonal edaphic changes. Cessation of shoot growth in mid-July corresponded to the period when soil salinity and soil temperatures were at high levels and soil moisture levels were at their lowest. Flowering began before shoot growth ceased and continued for some time after. The above ground portions of saltgrass plants died back by the end of August, leaving the rhizomes to prepare shoot buds for the next season. Although these phenological changes may be due to endogenous factors, work with saltgrass in controlled conditions suggests that environmental factors also play an important role.

5.3.2 Growth of tagged shoots

The significant difference in height of shoots between the short and tall growth forms of saltgrass was presumably due to some edaphic factor(s). The evidence for this is that both forms of saltgrass in the field experienced almost identical micrometeorological conditions, and growth in controlled conditions showed that height was not genetically limited. Many reports in the literature suggest that the saltgrass growth forms are responses to total soil salinity (Ungar 1965, 1967, 1968, 1970, Ungar et al. 1969). However, at Akasu Lake there was very little difference between saturation extracts of soils under short and tall saltgrass with respect to ECe, TC, % salts, and cation concentrations and ratios (see Tables 14 to 16). Since the ratio of SP to Pw was very close for both soils, concentrations at field moisture levels would probably be similar in both soils. The major difference between the two soils was in moisture levels. Soil of the tall Ds zone almost always had a higher moisture content than soil of the short Ds zone. Plants in the former zone were probably able to grow taller in the presence of this additional moisture.

5.3.3 Flowering percentage

The low total flowering percentages (17 to 18%) for both short and tall *Distichlis stricta* in 1977 and 1978 suggest that sexual reproduction is not as important to this species as vegetative reproduction. Although each panicle may produce several seeds, the seeds are fairly heavy and not likely to travel far. However, the rhizomes, which are often up to 180 cm in length, are well adapted to extending stands of saltgrass (Hansen et al. 1976). They can spread from areas favorable to growth to areas where salinity is higher. When conditions ameliorate, adventitious roots can form and new shoots will be produced.

5.4 Solution Culture Studies

5.4.1 Experiment 1

5.4.1.1 Growth of plants

The saltgrass plants used in this experiment were obtained from the short Ds zone at Akasu Lake. The heights they reached in solution culture were considerably greater than the average heights reached by short and tall saltgrass in the field. This shows that the growth reduction of the short form in the field is apparently not genetically controlled, for when these same plants are placed in favorable conditions they can grow vigorously.

None of the cation ratios used was adverse enough to cause a significant decrease in shoot or root dry weight of the plants. This suggests that saltgrass plants can adjust readily to a wide range of conditions. It is difficult to explain why plants in treatment solution 3 had the lowest number of shoots, shoot height, and dry weight of the four treatments, while plants in the less favorable solution 4 grew more vigorously than those in treatment 3. Since the differences were not significant, they may have been due to plant variability rather than to solution conditions. As Trelease and Livingston stated in 1924 with respect to growing plants in solution cultures, "internal variability is generally found to be far from negligible."

5.4.1.2 Tissue analyses

Cation concentrations in shoots and roots of saltgrass grown in the four solutions show that the plants were regulating tissue ion contents so that they fell within a range favorable to growth. When solution calcium concentrations decreased by a factor of eight, tissue calcium content fell by a factor of only three in the shoots and only two in the roots. Calcium uptake by the plants compared to solution calcium concentration was actually increased on a relative scale when solution concentrations dropped.

Likewise, the increase in tissue magnesium concentration was not proportional to the increase in solution magnesium concentration. The plants were somehow restricting magnesium content in the tissue so that it was present in a fairly narrow range of concentrations.

Tissue sodium concentrations were kept within the same maximum range as calcium and magnesium concentrations, with none of the three exceeding 0.3 me/g. In contrast, potassium concentrations were always above 0.3 me/g in shoot and root tissue, and reached as high as 0.5me/g. Considering the extremely low levels of potassium present in the nutrient solutions, it must be concluded that saltgrass roots were actively absorbing potassium by some high affinity mechanism and transporting it to the shoots.

The total cation concentration in plant tissue was held fairly constant in the four treatments; it varied from

0.9 to 1.1 me/g in shoot tissue and from 0.8 to 1.1 in root tissue. This probably falls within a range which is optimal for saltgrass growth.

Although there were significant differences between treatments with respect to tissue Mg/Ca ratio, the increase in tissue Mg/Ca from treatment 1 to 4 was far from being directly proportional to that in the solutions. Root Mg/Ca ratios were higher than shoot ratios, and exceeded the two lowest solution ratios. However, at the high solution Mg/Ca ratio, the root ratio was less than half and the shoot ratio less than one quarter of the solution ratio. The plants were apparently controlling the internal ratio by excluding magnesium from the shoots.

The cation to total cation ratios show the importance of potassium in shoot and root tissue. The K/TC ratios were from 2.2 to 2.6 times larger than the Na/TC ratios in the shoots, and from 1.5 to 1.7 times larger than Na/TC in the roots. These plants must require or prefer high K rather than high Na concentrations, perhaps for use in osmotic adjustment to high salinity.

Sodium concentrations and Na/TC ratios were always lower in shoots than roots, suggesting that the plants were restricting root to shoot Na transport, or excreting Na from the leaves. The importance of the latter in this experiment is not known, since the activity of salt glands was not investigated.

Comparison of data from this experiment with data from other studies is given in Tables 17 and 18. Due to space limitations, only shoot data are presented. Cation concentrations in general were much lower for saltgrass in this experiment than for many other plants grown under various conditions. In particular, tissue cation concentrations of *D. stricta* from Death Valley (Hunt and Durrell 1966) were much higher than those of saltgrass grown in solution culture, no doubt because substrate concentrations were much higher. However, the cation proportions were much different in the Death Valley plants than in the solution grown plants of Experiment 1. The relative concentration of sodium and potassium was reversed in the former plants; sodium greatly exceeded potassium in concentration and proportion of total shoot cations. This was also shown in saltgrass from Utah (Wiebe and Walter 1972, Hansen et al. 1976). It is difficult to explain this discrepancy, since it is such a complete reversal. The Utah and Death Valley plants may belong to different ecotypes than Akasu Lake plants, and the cation differences may be due to ecotypic variation. Soil type may also be important, since the Utah saltgrass plants grow on soils high in chlorides, while the Alberta plants grow on soils high in sulfates. Preparation of the tissue can also affect results of analyses, since washing is necessary to remove surface accumulations of ions secreted from salt glands.

A preference of potassium to sodium has been shown in many halophytes. Beadle et al. (1957) found that in some

Table 17. Calcium and magnesium concentration ranges (in me/g) in shoots of various plant species grown at constant or uncontrolled salinity levels.

Plant species	Conditions	Conc. range	Reference
		Calcium	
Several monocots	normal growth	0.29 - 0.88	Chapman 1966
Distichlis stricta	native soil, Death Valley	0.55 - 1.70	Hunt & Durrell 1966
Atriplex spp.	native soil, Australia	0.15 - 0.95	Beadle et al. 1957
11 salt desert plants	native soil, Utah	0.27 - 1.20	Cook et al. 1959
Agrostis stolonifera	50% seawater, + or - inundation	0.17 - 0.32	Rozema & Blom 1977
Juncus gerardii	as above	0.21 - 0.29	Rozema & Blom 1977
Barley	solution culture, 8 me/l Na, Mg/Ca 0.60 to 16.5	0.26 - 0.09	Carter 1977
Barley	solution culture, 90 me/l Na, Mg/Ca 0.75 to 7.75	0.17 - 0.09	Carter 1977
Distichlis stricta	solution culture, 100 me/l Na, Mg/Ca 1 to 15	0.23 - 0.07	L'Hirondelle
		Magnesium	
Several monocots	normal growth	0.08 - 0.43	Chapman 1966
Distichlis stricta	native soil, Death Valley	0.75 - 1.25	Hunt & Durrell 1966
Agrostis stolonifera	50% seawater, + or - inundation	0.11	Rozema & Blom 1977
Juncus gerardii	as above	0.11 - 0.12	Rozema & Blom 1977
Barley	solution culture, 8 me/l Na, Mg/Ca 0.60 to 16.5	0.20 - 0.87	Carter 1977
Barley	solution culture, 90 me/l Na, Mg/Ca 0.75 to 7.75	0.16 - 0.64	Carter 1977
Distichlis stricta	solution culture, 100 me/l Na, Mg/Ca 1 to 15	0.19 - 0.31	L'Hirondelle

Table 18. Sodium and potassium concentration ranges (in me/g) in shoots of various plant species grown at constant or uncontrolled salinity levels.

Plant species	Conditions	Conc. range	Reference
	Sodium		
Several grasses	soil growth	0.008 - 0.045	Griffith & Walters 1966
Distichlis stricta	native soil, Death Valley	2.30 - 4.00	Hunt & Durrell 1966
Distichlis stricta	native soil, Utah	0.43 - 1.10	Hansen et al. 1976
Atriplex spp.	native soil, Australia	1.96 - 3.40	Beadle et al. 1957
Sarcobatus vermiculatus	native soil, Utah	up to 4.35	Rickard 1965
Eurotia lanata	native soil, Utah	0.03	Moore et al. 1972
Atriplex confertifolia	native soil, Utah	3.70	Moore et al. 1972
Agrostis stolonifera	50% seawater, + or - inundation	0.28 - 0.39	Rozema & Blom 1977
Juncus gerardii	as above	0.69 - 1.15	Rozema & Blom 1977
Barley	solution culture, 50 me/l Na, low to high nutrients	0.50 - 1.00	Greenway 1963
Barley	solution culture, 8 me/l Na, Mg/Ca 0.60 to 16.5	0.32 - 0.95	Carter 1977
Barley	solution culture, 90 me/l Na, Mg/Ca 0.75 to 7.75	1.17 - 2.42	Carter 1977
Distichlis stricta	solution culture, 100 me/l Na, Mg/Ca 1 to 15	0.16 - 0.19	L'Hirondelle
	Potassium		
Several monocots	normal growth	0.11 - 1.20	Chapman 1966
Several grasses	soil growth	0.54 - 1.20	Griffith & Walters 1966
Corn	critical content	1.00	Walter & Peck 1975
Distichlis stricta	native soil, Death Valley	0.70 - 0.80	Hunt & Durrell 1966
Distichlis stricta	native soil, Utah	0.25 - 0.50	Hansen et al. 1976
Atriplex spp.	native soil, Australia	0.38 - 1.40	Beadle et al. 1957
Grayia apinosa	native soil, Utah	up to 2.56	Rickard 1965
Eurotia lanata	native soil, Utah	0.70	Moore et al. 1972
Atriplex confertifolia	native soil, Utah	0.90	Moore et al. 1972
Agrostis stolonifera	50% seawater, + or - inundation	0.36 - 0.48	Rozema & Blom 1977
Barley	solution culture, 50 me/l Na, low to high nutrients	0.25 - 0.75	Greenway 1963
Barley	solution culture, 8 me/l Na, Mg/Ca 0.60 to 16.5	1.14 - 0.91	Carter 1977
Barley	solution culture, 90 me/l Na, Mg/Ca 0.75 to 7.75	0.60 - 0.28	Carter 1977
Distichlis stricta	solution culture, 100 me/l Na, Mg/Ca 1 to 15	0.35 - 0.46	L'Hirondelle

species of *Atriplex* even though concentrations of Na were higher than K in leaf tissue, K/Na ratios in the plant were considerably higher than those in the soils in which the plants were growing. Even when K/Na in the soil was 1/131, the uptake of K was not greatly suppressed, suggesting that the plant must have a high affinity potassium uptake mechanism. *Eurotia lanata*, growing in Utah, accumulated potassium from 1.6 to 2.4 times greater than sodium. This also suggests the existence of a special potassium uptake mechanism. Albert and Popp (1977) gave evidence which strongly suggested that grasses and sedges as a group tend to have a greater preference for potassium than sodium, while some dicots (especially Chenopodiaceae) accumulate sodium in preference to potassium. Secretions from salt glands of grasses show that sodium is secreted in much greater proportions than potassium, which tends to be retained by the cells (Hansen et al. 1976, Ramati et al. 1976). These studies indicate that many grasses and grasslike plants have adapted to high salinities by excluding sodium and actively absorbing potassium.

The ability of saltgrass to maintain relatively low Mg/Ca ratios in tissue would be advantageous in preventing magnesium toxicity and/or calcium deficiency. Saltgrass plants in this study, grown in solutions where Mg/Ca ranged from 1 to 15, had shoot Mg/Ca of 1 to 4. Even lower Mg/Ca (0.08) was found in saltgrass plants in Utah (Wiebe and Walter 1972). This adaptation has been shown in serpentine plants, which grow on substrates with very high magnesium contents. Walker et al. (1955) found that when soil Mg/Ca was varied from 15 to 0.2, the Mg/Ca ratio in plant tissue of native serpentine species varied from 3.1 to 0.3. These plants were able to absorb enough Ca relative to Mg to prevent calcium deficiency symptoms, while crop plants grown in the same conditions died or suffered from Ca deficiency.

The ability of saltgrass to regulate internal ion concentrations when grown in adverse conditions is readily seen when compared to the growth of barley under similar conditions. Carter (1977) found that increasing Mg/Ca ratios with constant sodium concentrations in nutrient solutions resulted in decreased Ca and K concentrations and greatly increased Mg and Na concentrations in barley tissue. Internal Mg/Ca ratios as high as 10 were reached in barley shoots, and yields were considerably depressed. Carter suggested that barley was not able to absorb enough calcium to promote K uptake and Na exclusion. In saltgrass, even when tissue Ca/TC was low, sodium content did not increase significantly. It appears that Ca/TC is not as crucial in controlling ion selectivity in saltgrass as it is in glycophytes, or the calcium levels required are much lower.

5.4.2 Experiment 2

5.4.2.1 Growth of plants

Although increased sodium sulfate salinity did not significantly decrease growth of saltgrass plants in this experiment, the overall survival and growth of plants was less than that in Experiment 1. This could be partially due to the different means of obtaining shoots for the two experiments. The rhizomes collected from frozen soil for Experiment 2 had been subjected to much harsher conditions than those kept in the cold room for Experiment 1. In addition to this, plants in Experiment 2 were transferred from vermiculite with distilled water into concentrated culture solutions, while those in Experiment 1 were first allowed to sprout and grow for a short time in the soil in which they had been collected. The latter plants were probably not subjected to as great a shock in salt concentration as were the plants in Experiment 2.

Although the decreases in dry weight of plants from treatment A1 to B3 were not significant, it is possible that increasing salinity was responsible for the trend of decreased yields. The death of entire replicates only in the highest salt concentrations also suggests that increasing salinity influenced survival and growth of saltgrass. However, there is no statistical evidence that saltgrass grows best at low salinities; the determination of the optimum salt concentration for saltgrass growth apparently requires a much greater range of salinity. *Distichlis stricta* did not require added sodium for healthy growth of shoots and roots. The possibility that it requires sodium as a microelement was not ruled out, because sodium was likely present in impurities in the chemicals and water used in the solutions, and may also have been present in the rhizomes.

Shoot water content and succulence were slightly, but not significantly, decreased by increasing salinity. Plants even in the most concentrated solution had water contents greater than 250%. This is much higher than the water content of 99% reported for *Distichlis stricta* in native soil (Al-Saadi and Wiebe 1973). This lower value may be due to adverse field conditions or a different growth stage of the plant. Tiku (1976) found water content decreased from 200 to 114% in saltgrass when osmotic potentials in solution were lowered from 0 to -3200 kPa by adding NaCl. The succulence values reported by Tiku were 3.0 to 2.2 over the same osmotic potential range, compared with 3.9 to 3.6 over a range of -270 to -970 kPa as found in this study. These differences may be due to the different anions used (chloride vs. sulfate) or the different growing conditons (greenhouse vs. growth chamber).

The death of all barley plants except those in the control treatment indicates that these solutions were too concentrated for survival of nonhalophytic plants. The rapid growth of control barley plants showed that the control nutrient solution was adequate for normal growth, and that the environmental conditions in the growth chamber were favorable to barley growth.

5.4.2.2 Water potential measurements

Saltgrass plants were able to maintain a substantial water potential gradient between solution and plant in all the solutions used. Leaf water potential was at least 280 kPa lower than solution water potential in each treatment. There was little change in leaf water potential over the -270 to -440 kPa solution change, but the drop of solution osmotic potential to -970 kPa caused leaf water potential to decrease by an additional 400 to 500 kPa to -1200 kPa. Potassium ions may be important in lowering tissue water potentials, since they are absorbed in greater quantities than any other cations.

Other studies show that *Distichlis stricta* can maintain low leaf osmotic potentials to survive in saline soils. Harris et al. (1924) found that saltgrass in Utah had high leaf fluid concentrations which resulted in osmotic potentials of from -2000 to -4100 kPa. They suggested that the presence of very high chloride ion concentrations was mainly responsible for the high conductivity of leaf tissue fluids. Dodd and Coupland (1966a) measured leaf sap osmotic potentials of saltgrass over the growing season in Saskatchewan, and found that OP ranged from -2170 to -4780 kPa, with a mean of -3040 kPa. ElSharkawi (1969) reported that saltgrass was able to adjust to salinity stress by increased osmotic adjustment, and was able to survive salinity stresses to -9000 kPa. Detling (1969) measured leaf water potential of saltgrass during the growing season in Utah, and found a range of -500 to -4000 kPa. When plants were greenhouse grown, leaf water potential varied from -270 to -4650 kPa depending on soil salt and water percentages. Tiku (1976) grew saltgrass in solutions in which osmotic potential was lowered from 0 to -3200 kPa by adding NaCl, and found that plant OP decreased from -1300 to -4700 kPa. The potentials recorded in Experiment 2 fall within the ranges reported in most of the above studies. Saltgrass is capable of adjusting to lower osmotic potentials than those to which it was subjected in solution culture in this study.

Other halophytes show similar patterns of osmotic adjustment to saline media. The leaf sap osmotic potentials of *Atriplex nummularia* and *A. inflata* were always considerably lower than solution osmotic potentials, even in the control solution; they fell as low as -5500 kPa for the former and -7400 kPa for the latter species when solution OP was -2400 kPa (Ashby and Beadle 1957). Leaf osmotic potentials of *A. halimus* grown in NaCl solution decreased rapidly with the initial drop in external OP, then remained fairly constant to about -900 kPa in the external solution (Gale and Poljakoff-Mayber 1970, Mozafar et al. 1970a). In *Spartina townsendii*, the osmotic potential of shoot sap paralleled the decreasing OP of the NaCl solution in which it was growing (Storey and Wyn Jones 1978b).

The importance of the potassium ion in contributing to osmotic adjustment has been discussed by Rozema (1975b, 1976). In *Juncus* species and *Glaux maritima*, potassium was responsible for a large part of the leaf sap OP, expecially at low salinities. As salinity increased, K concentration in leaf sap remained fairly constant in the *Juncus* species, but the contribution of Cl and Na to osmotic potential increased. At most salinities, Na, K and Cl accounted for 75 to 80% of the OP of plant sap. Wallace and Kleinkopf (1974) also found that Na and K accounted for most of the water potential in halophyte species. In other halophytes, organic compounds such as glycinebetaine may be more important in lowering plant OP (Storey and Wyn Jones 1978b). Albert and Popp (1977) suggested that accumulation of sugars in halophytic grasses is largely responsible for their low cell sap osmotic potentials. It is not known to what extent organic solutes contribute to leaf osmotic potential in *Distichlis stricta*, but in view of the relatively low tissue cation concentrations shown in these experiments, organic solutes and potassium are probably responsible for the major portion of leaf OP.

One factor involved in maintaining favorable plant water relations is relative humidity. Several authors have found that high relative humidities can greatly relieve the suppressive effect of salinity, so that salt tolerance of plants can increase without significantly changed tissue ion contents (Nieman and Poulsen 1967, Gale et al. 1970, Hoffman and Rawlins 1971, Hoffman and Jobes 1978). The low relative humidities (RH) used in the foregoing studies were generally about 45%, while the high ones were 85 to 100%. The RH used in the growth chamber experiments of this study was 63%, which is about halfway between the above values. This RH could have lessened salt stress compared to that at a lower RH, thus keeping yields fairly high. It must be remembered that this RH is the average low found at the Akasu Lake site, so the saltgrass plants used were probably adapted to this level of humidity. Use of a lower RH in combination with salinity might have affected growth differently.

5.4.2.3 Tissue analyses

Cation concentrations and ratios in saltgrass tissue indicated that the plants were responding to external concentrations, but were regulating uptake to keep ions in favorable balance in the tissues.

Calcium concentrations were very different in plants grown in solutions with two different Ca levels. The difference between A and B plants was maintained at all salinity levels. The Ca contents of plants in the B and C groups (30 and 8 me/l solution Ca respectively) were higher than any reached in Experiment 1, including the treatment at 40 me/l solution Ca. This difference may be related to plant variability.

Tissue magnesium concentrations changed very little with increasing salinity, and remained at fairly low levels in all treatments. The Mg concentrations in this experiment were comparable to those in Experiment 1.

In the plants which survived to the end of the experiment, the tissue sodium content was low compared to the ones which succumbed early. The death of plants in A3 and B3 may have been partly due to their inability to exclude and/or excrete sodium at high external concentrations. The presence of sodium in control plant tissue may have been due to solution contamination and/or to inherent sodium concentration in the rhizomes from which plants were started. To eliminate the latter source, it would be necessary to propagate plants over several generations in sodium free culture solutions.

The sodium concentrations in plants grown in 50 to 100 me/l Na were comparable to those found in plants grown in 100 me/l Na in Experiment 1. In A3 (300me/l Na), the high shoot Na content was not significantly different from that of other A or B treatments, but the root concentration was significantly greater than that of all other treatments. The roots probably lost some of their ability to exclude sodium at this high concentration, but the plant was able to keep Na content low in the shoots, probably by excretion from salt glands.

The increase in sodium concentration in the root medium seems to have caused decreased root potassium uptake, but the differences between treatments were not significant. Shoot K concentrations were considerably higher than root concentrations, and in most cases were higher than K concentrations of plants in Experiment 1. It is possible that the roots were actively absorbing K and transporting it to the shoots, but were also losing some root K back to the external solution due to increased salinity and perhaps some loss of membrane integrity with respect to monovalent ions. Greenway (1963) found that barley grown in high salinity, low nutrient solutions lost a significant portion of K back to the substrate.

The very low potassium concentration of tissue in treatment B3 is correlated with the early death of these plants, but whether it is a cause or a result of tissue death is difficult to determine. In either case, saltgrass plants grown in high salt concentrations seem to require high internal potassium concentrations for survival. These concentrations may be necessary for osmotic adjustment or for maintaining metabolism under adverse conditions.

Total cation concentrations of saltgrass plants in Experiment 2 were remarkably similar to those in Experiment 1, considering the differences in solution composition and concentration between the two experiments. There were no significant differences in shoot TC over a solution range of 18 to 368 me/l in Experiment 2. Root TC was more varied, but was even lower than shoot TC. These plants were able to regulate total ion uptake and ion excretion such that tissue TC fell within a fairly narrow range of optimum concentrations. This constancy of tissue TC suggests that although ion uptake may be important in osmotic adjustment of saltgrass, it is not the major factor involved in lowering tissue osmotic potential. The TC of shoots in the control (grown in a solution of -60 kPa) was about the same as that in A3 (grown in -970 kPa), but their shoot water potentials were very different (-510 vs -1250 kPa). Synthesis and accumulation of organic solutes must be responsible for this drop in shoot water potential.

The striking differences in tissue Mg/Ca ratios between A and B treatments were due to the differences in Ca concentration between the two groups. Because Ca contents were higher in roots than in shoots for the B treatments, their Mg/Ca ratios were lower in roots than in shoots. The reverse was true for the A treatments. The tissue Mg/Ca ratios in this experiment were similar to those in Experiment 1.

The cation to total cation concentration ratios clearly illustrate the dominance of potassium over sodium in the shoots of all plants which survived the high salinities. The tissue K/TC ratios were similar to those of Experiment 1. Magnesium proportions changed very little among treatments, while calcium proportions reflected their solution ratios. Even when solution Ca/TC was as low as 0.02 and K/TC was 0.01, the plants were able to survive and grow, and were successful in maintaining favorable ion proportions in shoot tissue. The plants which did not survive (B3) had the lowest K/TC and highest Na/TC of any treatment, even though their Ca/TC ratios were high. This suggests that perhaps a favorable K/TC, and not Ca/TC is crucial to survival in this species. This is supported by the results of the correlation test, which showed that K/TC was significantly correlated with both root and shoot dry weight, while there were no significant correlations with Ca/TC.

Comparison of saltgrass and barley tissue analyses shows how effective saltgrass was in controlling ion concentrations. All cation concentrations, especially sodium, tended to be much greater in barley tissue than saltgrass tissue. The highest sodium concentration in saltgrass tissue, in the dead plants of B3, was 0.78 me/g, while in barley it was as high as 6.2 in the shoots and 2.3 in the roots. Barley was not able to restrict entry of excess ions when grown in these high salt concentrations. This has been found in other studies (Greenway 1963, Carter 1977).

Tables 19 and 20 present cation concentration data obtained in other plant studies using several salinity levels. Most of the saltgrass concentrations tend to be among the lower ones found in plants grown in solutions with added sodium, although potassium concentrations are medium to high when compared with those of other halophytes.

Other studies with saltgrass have shown that it is able to survive at high salt concentrations, but does not necessarily prefer them. Harris et al. (1924) stated that saltgrass had inherently higher concentrations than some other grass species, and that these concentrations were not determined solely by the environment in which it was

Table 19. Calcium and magnesium concentration ranges (in me/g) in shoots of various plant species grown at increasing salinity levels. The directions of concentration ranges correspond to the directions of the salinity gradients. ESP = exchangeable sodium percentage.

Plant species	Conditions	Conc. range	Reference
	Calcium		
Beans, beets, etc.	sand-resin culture, ESP 0 to 75%	0.75 - 0	Bower & Wadleigh 1948
Wheat	sand-resin culture, ESP 15 to 60%	0.22 - 0.05	Abrol 1968
Serpentine plants	soil, Mg/Ca 0.2 to 15, %Ca 82 to 6	1.13 - 0.32	Walker et al. 1955
Glaux maritima	solution culture, 0 to 300 me/l NaCl	0.35 - 0.45	Rozema 1975b
Juncus spp.	as above	0.13 - 0.03	Rozema 1976
Chloris gayana	sand culture, 0 to 200 me/l NaCl	1.60 - 1.00	Guggenheim & Waisel 1977
Agropyron elongatum	solution culture, 0 to 500 me/l NaCl	1.15 - 0.33	Elzam & Epstein 1969a
Distichlis stricta	solution culture, 0 to 300 me/l Na, Mg/Ca 1 to 5	0.35 - 0.08	L'Hirondelle
	Magnesium		
Beans, beets, etc.	sand-resin culture, ESP 0 to 75%	0.90 - 0.05	Bower & Wadleigh 1948
Wheat	sand-resin culture, ESP 15 to 60%	0.05 - 0.08	Abrol 1968
Serpentine plants	soil, Mg/Ca 0.2 to 15, %Ca 82 to 6	1.00 - 0.31	Walker et al. 1955
Glaux maritima	solution culture, 0 to 300 me/l NaCl	0.13 - 0.17	Rozema 1975b
Juncus spp.	as above	0.04 - 0.08	Rozema 1976
Chloris gayana	sand culture, 0 to 200 me/l NaCl	1.10 - 0.80	Guggenheim & Waisel 1977
Distichlis stricta	solution culture, 0 to 300 me/l Na, Mg/Ca 1 to 5	0.18 - 0.22	L'Hirondelle

Table 20. Sodium and potassium concentration ranges (in me/g) in shoots of various plant species grown at increasing salinity levels. The directions of concentration ranges correspond to the directions of the salinity gradients. ESP = exchangeable sodium percentage.

Plant species	Conditions	Conc. range	References
		Sodium	
Beans, beets, etc.	sand-resin culture, ESP 0 to 75%	0 - 3.00	Bower & Wadleigh 1948
Wheat	sand-resin culture, ESP 15 to 60%	0.43 - 1.74	Abrol 1968
Atriplex nummularia	solution culture, 50 to 600 me/l Na	0.01 - 5.90	Ashby & Beadle 1957
Atriplex inflata	as above	0.02 - 7.10	Ashby & Beadle 1957
Atriplex vesicaria	solution culture, 0 to 1000 me/l NaCl	0.07 - 7.00	Black 1960
Atriplex spongiosa	solution culture, 0 to 800 me/l NaCl	1.00 - 7.00	Storey & Wyn Jones 1979
Suaeda monoica	as above	1.00 - 8.00	Storey & Wyn Jones 1979
Agropyron elongatum	solution culture, 1 to 400 me/l NaCl	0 - 2.00	Greenway & Rogers 1963
Agropyron elongatum	solution culture, 0 to 500 me/l NaCl	0.01 - 3.30	Elzam & Epstein 1969a
Agrostis stolonifera	solution culture, 0 to 217 me/l NaCl	0.07 - 1.23	Tiku & Snaydon 1971
Spartina foliosa	seawater, 0 to 100%	0.10 - 2.00	Phleger 1971
Glaux maritima	solution culture, 0 to 300 me/l NaCl	0.13 - 0.78	Rozema 1975b
Juncus spp.	as above	0.02 - 0.15	Rozema 1976
Chloris gayana	sand culture, 0 to 200 me/l NaCl	0.20 - 1.10	Guggenheim & Waisel 1977
Distichlis stricta	solution culture, 0 to 1000 me/l NaCl	0.01 - 0.71	Tiku 1976
Distichlis stricta	solution culture, 0 to 300 me/l Na, Mg/Ca 1 to 5	0.05 - 0.42	L'Hirondelle
		Potassium	
Beans, beets, etc.	sand-resin culture, ESP 0 to 75%	1.50 - 0.25	Bower & Wadleigh 1948
Wheat	sand-resin culture, ESP 15 to 60%	1.00 - 0.25	Abrol 1968
Atriplex nummularia	solution culture, 50 to 600 me/l Na	2.00 - 0.27	Ashby & Beadle 1957
Atriplex inflata	as above	2.10 - 0.29	Ashby & Beadle 1957
Atriplex vesicaria	solution culture, 0 to 1000 me/l NaCl	1.00 - 0.25	Black 1960
Atriplex spongiosa	solution culture, 0 to 800 me/l NaCl	1.80 - 0.25	Storey & Wyn Jones 1979
Suaeda monoica	as above	0.80 - 0.40	Storey & Wyn Jones 1979
Serpentine plants	soil, Mg/Ca 0.2 to 15, %Ca 82 to 6	1.08 - 0.99	Walker et al. 1955
Agropyron elongatum	solution culture, 1 to 400 me/l NaCl	1.50 - 1.00	Greenway & Rogers 1963
Agrostis stolonfera	solution culture, 0 to 217 me/l NaCl	0.02 - 0.18	Tiku & Snaydon 1971
Spartina foliosa	seawater, 0 to 100%	0.88 - 0.50	Phleger 1971
Glaux maritima	solution culture, 0 to 300 me/l NaCl	0.36 - 0.08	Rozema 1975b
Juncus spp.	as above	0.15 - 0.08	Rozema 1976
Chloris gayana	sand culture, 0 to 200 me/l NaCl	0.40 - 0.20	Guggenheim & Waisel 1977
Distichlis stricta	solution culture, 0 to 300 me/l Na, Mg/Ca 1 to 5	0.65 - 0.44	L'Hirondelle

growing. This does not agree with the results of Experiment 1 and 2. This difference may be related to the presence of high Cl concentrations in the soils in Utah where saltgrass was growing, as opposed to sulfate in the solution cultures. Ecotypic variation may also cause different plant responses.

Ahi and Powers (1938) found that saltgrass yields were greater in cool than warm temperatures, and were decreased considerably by increasing salinity from 1 to 8% of seawater. Adams (1963) found that *Distichlis spicata* from North Carolina, the closely related coastal species, grew better in 1% NaCl than 0 or 2% NaCl, and he suggested that this species was an obligate halophyte. Barbour and Davis (1970) who grew the coastal species from California, found that it did best in the low (0.1%) salt concentration and poorest in the high (1.1%) salt concentration. Detling (1969) remarked upon the low salt concentrations in saltgrass leaves from Utah, compared with those of *Sarcobatus vermiculatus*, *Suaeda fruticosa* and *S. depressa*. He believed that this indicated saltgrass was able to exclude excess salts, enabling it to tolerate high salt concentrations. Tiku (1976), who found that sodium concentration in *D. stricta* grown with added NaCl was 3 to 5.5 times lower than that in *Salciornia rubra* grown under the same conditions, suggested that saltgrass is adversely affected by NaCl.

The above studies suggest that there may be several ecotypes of *Distichlis stricta*, each adapted to different optimum growth conditions, and related by their ability to survive in salt concentrations which limit or prevent growth of other species. The dominant anion (sulfate or chloride) present in the environment may strongly influence ion relations in saltgrass. This may explain the discrepancies in tissue ion contents between this study, where a sulfate system was used, and other studies, where chloride was dominant. It is not likely that saltgrass is an obligate halophyte, since it usually grows best at low salinities. Barbour (1970b) feels that there is as yet no conclusive evidence that any angiosperm is an obligate halopyte. According to his definition, saltgrass would be a facultative halophyte.

5.4.3 Survival strategy of saltgrass

A striking feature of the behavior of *Distichlis stricta* in solution culture in this study is its ability to accumulate potassium and exclude sodium from plant tissues. Selective K accumulation has been reported in other halophytes (Albert and Popp 1977). There appears to be a high affinity mechanism responsible for K uptake at low solution K concentrations and high solution Na concentrations. This mechanism is probably independent of Na concentration, thus enabling the plant to absorb large quantities of K without appreciable Na competition. The absorbed K may function in osmotic adjustment and enzymatic reactions.

The exclusion of high salt concentrations from plant tissues appears to be the mechanism enabling saltgrass to survive in high salinities. Even in barley, the ability to regulate ion content has been found to be an important characteristic of salt tolerant varieties (Greenway 1962, 1973). In salt tolerant clones of *Festuca rubra* and *Agrostis stolonifera*, the total tissue ion concentrations could be kept at half those of nontolerant clones by exclusion at high salinities, and tolerance was associated with maintenance of almost constant ion concentrations in roots over the complete salinity range (Hannon and Barber 1972). The results of the saltgrass solution culture experiments are quite similar to those for *Festuca* and *Agrostis*.

It has been suggested that salt accumulators are able to grow more vigorously at high salt concentrations than salt excluders (Greenway and Osmond 1970), but salt exclusion can be a very effective means of survival. The low internal salt status of salt excluders is beneficial in terms of maintaining enzymatic reactions, and salt excluders can adjust to high salinities readily by synthesizing large quantities of sugars (Albert and Popp 1977). The results from the solution culture experiments with saltgrass show that it is a successful excluder. It is probably also a successful excretor since it has salt glands which secrete large proportions of Na to K (Hansen et al. 1976).

The widespread distribution of some halophytes may be explained by the occurrence of several ecotypes (Goodman

1973). There are probably several ecotypes of saltgrass, which may explain the variation in salt tolerance and tissue ion concentrations among plants from different locations. Previous studies have dealt with saltgrass from sodium chloride substrates, while this study used saltgrass from a sodium sulfate substrate.

The occurrence of saltgrass in saline conditions which are not always optimum for its growth may be due to lack of competition at those salinities. Where the short growth form is dominant, few other species can survive. Other authors have suggested that competition plays an important role in resticting halophytes to areas of high salinity (Phleger 1971, Barbour 1978, Ungar et al. 1979).

5.5 Germination

Germination of saltgrass seeds was affected by both decreasing osmotic potential and type of salt. The sodium salts, which occur naturally in large quantities in soils where saltgrass is found, were least inhibitory to germination, while the magnesium salt and PEG, a non-permeating solute, were most inhibitory to germination. Other studies have shown that magnesium salts are more inhibitory than sodium salts (Hyder and Yasmun 1972) and that nonpermeating solutes are more inhibitory than salts (Macke and Ungar 1971).

At high osmotic potentials (0 or -200 kPa) maximum germination occurred, and as osmotic potentials decreased germination dropped sharply at first, then gradually to zero. There was no significant difference between germination at 0 and -200 kPa; this small amount of added salt was neither stimulatory or inhibitory. The drop in germination at OPs from -200 to -500 kPa was sharper than the drop from -500 to -1000 in all osmotica. There is apparently not a very large gradient over which salts become inhibitory. This has been shown in other studies (Ungar 1962, Macke and Ungar 1971).

The maximum percent germination obtained in this experiment was lower than that obtained by Nielson (1956) using *Distichlis stricta* seeds from Utah. He found that sandpaper scarification gave germination up to 72% in distilled water. It is not known why germination percentage for the Akasu Lake seeds was so low.

Other studies on halophyte germination indicate that while low salt concentrations may stimulate germination in some species, salt is not required for germination, and germination is usually highest at low salinities (Hogan 1968, Ungar and Capilupo 1969, Ungar and Hogan 1970, Macke and Ungar 1971, Williams and Ungar 1972, Ungar 1974c, 1977). *Distichlis stricta* seeds fit this pattern. They are not inhibited by low salt concentrations, but are greatly inhibited as salt concentration increases. They are obviously adapted to germinate at a time when salinities are low, most likely in early spring.

It is impossible to say for certain whether the salts used were toxic to saltgrass seeds, because mold formation was responsible for death of many seeds. However, it seems likely that some osmotica, especially PEG, have toxic effects which cannot be removed by soaking seeds in distilled water.

6. CONCLUSIONS

Both the ecological and physiological aspects of this study showed that *Distichlis stricta*, saltgrass, is a halophyte due to increased competitive advantage in saline soils, and not because it requires high salinities for optimum growth.

Analyses of soils from under saltgrass plants near Vegreville, Alberta showed that the densest stands of saltgrass (short Ds) were found on soils with the highest salinities (high ECe, TC, and Mg/Ca), highest temperatures, and low soil moisture levels. These plants represented the short (dwarf) end of a gradient of plant height. Significantly taller and somewhat less dense saltgrass plants (tall Ds) were found on soils with higher moisture levels and lower soil temperatures than short Ds. Where soil salinity was considerably lower, tall saltgrass plants (tall, scattered Ds) were found widely scattered among other species. The height of saltgrass plants is affected by soil salinity, moisture, and temperature. Any combination of these soil conditions can reduce growth by increasing water stress, i.e. by lowering the soil water potential. In areas where soil moisture and temperature are relatively constant, increases in total soil salinity appear to be limiting to plant growth. Where soil salinity is relatively constant, low soil moisture and/or high soil temperatures can limit growth.

Saturation extracts of tall Ds soils were characterized by very low potassium concentrations (less than 1% of TC), low calcium (4 to 10% of TC), and very high magnesium and sodium concentrations (together 89 to 95% of TC). Although soils under tall, scattered Ds typically had four to five times lower TC than those above, the proportions of cations present were similar. Nearby samples of lake water also had low TC, but again magnesium and sodium accounted for 90 to 96% of TC.

Halophyte communities at Akasu Lake generally had low cover values and low species diversity. Twenty one plant species representing ten families were found. The species most frequently found with saltgrass were *Hordeum jubatum*, *Puccinellia nuttalliana* and *Suaeda calceoliformis*. *Hordeum* most successfully competed with saltgrass on soils of medium to low salinity and moisture. *Puccinellia* dominated on very moist, moderately saline soils, while *Suaeda* was found with the short form of *Distichlis* on very saline, moderately moist soils. Saltgrass had the highest percent cover on soils with high salinity and low moisture, where it could apparently outcompete other species.

The short period of active growth of saltgrass (about 8 to 10 weeks) was correlated with favorable microclimatic and edaphic conditions. When soil salt concentrations became high and soil moisture dropped in midsummer, the above ground portions of the plants ceased growth. Flowering percentages were low, suggesting that spreading by vegetative means (rhizomes) was more important than reproduction by seeds.

Growth chamber studies with saltgrass in solution culture showed that plants which were started from rhizomes of the short growth form were not inherently short, and could grow to "tall" heights when conditions were favorable. Although the nutrient solutions were based on soil cation concentrations and ratios, they were not as concentrated or variable as midsummer soil solutions and were therefore probably not as limiting to growth. Plants grown in a series of solutions with different sodium concentrations and Mg/Ca ratios did not significantly differ in dry weight, height, water content or succulence, showing that they were able to adjust readily to large external differences. Saltgrass also grew vigorously with no added sodium salts, which indicated that if sodium is required for growth it must be in very small amounts (there may have been sodium contamination as impurities in other nutrient salts or from endogenous sodium in the rhizomes).

The plants maintained water potential gradients between shoots and nutrient solutions (with differences ranging from 280 to 500 kPa) probably by means of accumulation of potassium and organic solutes.

Saltgrass plants in these solution culture experiments were able to regulate internal ion concentrations. Tissue TC was similar in all treatments, and was low compared to TC found in other halophyte species.

Plants grown in solutions with large differences in ion concentrations had different internal ion concentrations, but these differences were not in proportion to external ones. Tissue calcium concentrations were low, and reflected solution Ca/TC rather than solution calcium concentration. Magnesium and sodium concentrations were relatively low in shoot and root tissue, probably due to exclusion at root surfaces and excretion from leaf surfaces. Sodium concentrations were high only in plants which died early in the experiment, and potassium concentrations were very low in these plants. Healthy saltgrass plants had relatively high potassium contents, probably due to active uptake. Significant positive correlations were found between tissue dry weight and tissue potassium concentrations and K/TC ratios. Relatively large amounts of potassium were obviously crucial to survival and growth in saltgrass, and tissue K/TC was far more important than Ca/TC in favoring optimum growth. It is remarkable that there were such large differences between solution or soil K/TC and tissue K/TC. These plants must possess a very efficient mechanism of potassium uptake.

High single salt concentrations and corresponding low osmotic potentials greatly inhibited and delayed germination of saltgrass seeds. Slight additions of salt were neither stimulatory nor inhibitory. The two sodium salts (chloride and sulfate) were least inhibitory, and magnesium sulfate and PEG (a non-permeating solute) were most inhibitory to germination. There was no germination at -2000 KPa (-20 bars), so in nature these seeds must germinate when salt concentrations are low, most likely in early to late spring.

Some authors may not consider *Distichlis stricta* a true halophyte, since it does not require added sodium or high salt concentrations for optimum growth, and it does not tolerate high internal ion concentrations. It is in fact a salt excluder and/or excretor. However, it is able to successfully compete in saline soils. and does consistently complete its life cycle in this habitat, so according to the definition of Waisel (1972), it can be called a halophyte.

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APPENDICES

Appendices Abbreviations

SEM = standard error of mean

Ds = Distichlis stricta

DF = degrees of freedom

P = probability

SS = sum of squares

MS = mean square

S = shoots

R = roots

TC = total cation concentration

Ht = height

SWC = shoot water content

F Wt = fresh weight

D Wt = dry weight

E = error

* = significant at p less than 0.05

For experiment 2, X = Mg/Ca ratios (2 levels) and
Y = salt concentrations (3 levels)
Group 1 = 50 me/l Na, Group 2 = 100 me/l Na,
and Group 3 = 300 me/l Na

For detailed descriptions of groups from Experiments 1 and 2, see Tables 1 and 2 (pages 53 and 60).

Appendix 1: T-test comparison of shoot height of tall and short saltgrass plants.

	Mean height (cm) ± SEM	
Date measured	Short Ds	Tall Ds
May 26	4.37 ± 0.12	5.37 ± 0.17
June 2	5.30 ± 0.13	7.00 ± 0.19
June 10	6.52 ± 0.17	8.38 ± 0.28
June 16	6.93 ± 0.18	8.75 ± 0.29
June 23	7.12 ± 0.22	8.77 ± 0.31
June 30	7.43 ± 0.21	8.93 ± 0.31
July 7	7.31 ± 0.21	9.06 ± 0.31

		T-test comparison of means	
Date measured	DF	T	P
May 26	98	4.87	0.000*
June 2	97	7.26	0.000*
June 10	96	5.63	0.000*
June 16	95	5.22	0.000*
June 23	94	4.37	0.000*
June 30	93	3.94	0.000*
July 7	93	4.66	0.000*

Appendix 2: Short and tall saltgrass flowering percentages; raw data and t-test comparison of means.

Raw Data, Means and SEM

Year and growth form	Total # shoots	% Male flowers	% Female flowers	% Male + Female flowers
1977 short	98	3.1	5.1	8.2
	80	0	6.3	6.3
	56	16.1	5.4	21.4
	62	29.0	6.5	35.5
	74	1.4	18.9	20.3
	74 ± 7	9.9 ± 5.6	8.4 ± 2.6	18.3 ± 5.3
1977 tall	314	29.6	2.9	32.5
	88	2.3	4.6	6.9
	135	3.7	0	3.7
	80	22.5	0	22.5
	130	15.4	6.2	21.6
	149 ± 43	14.7 ± 5.3	2.7 ± 1.2	17.4 ± 5.3
1978 short	232	8.2	4.7	12.9
	230	6.1	10.9	17.0
	210	5.7	11.0	16.7
	205	7.3	10.7	18.0
	120	5.0	17.5	22.5
	199 ± 21	6.5 ± 0.6	11.0 ± 2.0	17.4 ± 1.5
1978 tall	155	3.9	5.8	9.7
	170	4.1	5.9	10.0
	185	17.3	6.0	23.2
	215	13.5	0.5	14.0
	115	26.1	0	26.1
	168 ± 17	13.0 ± 4.2	3.6 ± 1.4	16.6 ± 3.4

Appendix 2 (continued): Short and tall saltgrass flowering percentages; raw data and t-test comparison of means.

T-test Comparison of Means of Short and Tall Ds

Variable	DF	T	P
1977 data			
Total shoot number	8	1.75	0.119
% male flowers	8	0.62	0.550
% female flowers	8	1.96	0.086
% male + female flowers	8	0.12	0.907
1978 data			
Total shoot number	8	1.19	0.268
% male flowers	8	1.54	0.163
% female flowers	8	3.00	0.017*
% male + female flowers	8	0.22	0.830

Appendix 3: Experiment 1 growth variables; raw data and one-way analyses of variance.

Raw Data, Means and SEM

Treatment	Dry wt of shoots (gm)	Dry wt of roots (gm)	Shoot height (cm)	Number of shoots
1	2.14	2.16	16	41
	2.05	2.07	14	46
	1.39	1.12	11	36
	1.86 ± 0.24	1.78 ± 0.33	14 ± 1.5	41 ± 3
2	2.86	1.89	13	61
	1.94	2.59	15	33
	0.74	1.33	12	15
	1.85 ± 0.61	1.94 ± 0.36	13 ± 0.9	36 ± 13
3	0.92	1.11	11	22
	1.46	1.04	11	40
	0.83	1.22	11	26
	1.07 ± 0.19	1.12 ± 0.05	11 ± 0	29 ± 5
4	1.31	1.13	12	34
	2.27	1.66	14	61
	2.24	1.69	13	57
	1.94 ± 0.32	1.50 ± 0.18	13 ± 0.6	51 ± 8

Appendix 3 (continued): Experiment 1 growth variables; raw data and one-way analyses of variance.

One-way Analysis of Variance

Shoot Dry Weight

Source of variation	SS	MS	DF	F	P
Groups	1.51	0.50	3	1.18	0.378
Error	3.41	0.43	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	1.000	0.559	0.999
2		-	0.573	0.999
3			-	0.487
4				-

Root Dry Weight

Source of variation	SS	MS	DF	F	P
Groups	1.15	0.38	3	1.83	0.219
Error	1.67	0.21	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.981	0.426	0.896
2		-	0.269	0.715
3			-	0.803

Shoot Height

Source of variation	SS	MS	DF	F	P
Groups	12.9	4.31	3	1.78	0.228
Error	19.3	2.42	8		

F ratios matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.07	4.42	0.28
2		-	3.38	0.07
3			-	2.48
4				-

F must be greater than 12.21 for significance at $p < 0.05$

Appendix 3 (continued): Experiment 1 growth variables; raw data and one-way analyses of variance.

One-way Analysis of Variance

Number of Shoots

Source of variation	SS	MS	DF	F	P
Groups	721	240	3	1.11	0.399
Error	1728	216	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.984	0.814	0.882
2		-	0.950	0.708
3			-	0.421

Appendix 4: Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions.

Raw Data, Means and SEM

(Concentrations in me/g)

Treatment	[Ca] S	[Ca] R	[Mg] S	[Mg] R	[Na] S	[Na] R
1	0.129	0.083	0.113	0.137	0.190	0.274
	0.200	0.077	0.223	0.152	0.202	0.156
	0.372	0.070	0.226	0.185	0.167	0.189
	0.234	0.077	0.187	0.158	0.186	0.206
	± 0.072	± 0.004	± 0.037	± 0.014	± 0.010	± 0.035
2	0.104	0.048	0.222	0.206	0.230	0.308
	0.131	0.036	0.222	0.151	0.141	0.167
	0.147	0.078	0.213	0.192	0.108	0.217
	0.127	0.054	0.219	0.183	0.160	0.231
	± 0.013	± 0.013	± 0.003	± 0.017	± 0.036	± 0.041
3	0.154	0.045	0.386	0.225	0.259	0.325
	0.091	0.057	0.236	0.269	0.112	0.306
	0.114	0.052	0.303	0.259	0.191	0.232
	0.120	0.051	0.308	0.251	0.187	0.288
	± 0.018	± 0.003	± 0.043	± 0.013	± 0.043	± 0.028
4	0.080	0.039	0.243	0.266	0.188	0.281
	0.072	0.036	0.290	0.232	0.190	0.312
	0.067	0.029	0.223	0.207	0.168	0.251
	0.073	0.035	0.252	0.235	0.182	0.281
	± 0.004	± 0.003	± 0.020	± 0.017	± 0.007	± 0.018

Appendix 4 (continued): Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions.

Raw Data, Means and SEM

(Concentrations in me/g)

Treatment	[K] S	[K] R	[TC] S	[TC] R
1	0.458	0.407	0.890	0.901
	0.476	0.249	1.101	0.634
	0.368	0.359	1.133	0.803
	0.434	0.338	1.041	0.779
	± 0.033	± 0.047	± 0.076	± 0.078
2	0.408	0.336	0.964	0.898
	0.362	0.360	0.856	0.714
	0.282	0.420	0.750	0.907
	0.351	0.372	0.857	0.840
	± 0.037	± 0.025	± 0.062	± 0.063
3	0.466	0.540	1.265	1.135
	0.475	0.513	0.914	1.145
	0.435	0.429	1.043	0.972
	0.459	0.494	1.074	1.084
	± 0.012	± 0.033	± 0.103	± 0.056
4	0.476	0.491	0.987	1.077
	0.394	0.400	0.946	0.980
	0.479	0.346	0.937	0.833
	0.450	0.412	0.957	0.963
	± 0.028	± 0.042	± 0.015	± 0.071

Appendix 4 (continued): Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions.

One-way Analysis of Variance

Shoot Calcium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.042	0.01	3	3.23	0.082
Error	0.034	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.334	0.283	0.094
2		-	0.999	0.794
3			-	0.856
4				-

Root Calcium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.003	0.00	3	6.24	0.017*
Error	0.001	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.226	0.161	0.018*
2		-	0.994	0.338
3			-	0.453
4				-

Shoot Magnesium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.024	0.01	3	2.91	0.101
Error	0.022	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.906	0.119	0.547
2		-	0.299	0.895
3			-	0.646
4				-

Appendix 4 (continued): Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions.

One-way Analysis of Variance

Root Magnesium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.017	0.01	3	8.06	0.008*
Error	0.006	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.730	0.018*	0.047*
2		-	0.080	0.206
3			-	0.906
4				-

Shoot Sodium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.002	0.00	3	0.21	0.890
Error	0.020	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.931	1.000	1.000
2		-	0.923	0.957
3			-	0.999
4				-

Root Sodium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.014	0.00	3	1.54	0.278
Error	0.024	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.959	0.408	0.472
2		-	0.672	0.742
3			-	0.999
4				-

Appendix 4 (continued): Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions.

One-way Analysis of Variance

Shoot Potassium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.022	0.01	3	2.88	0.103
Error	0.020	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.322	0.946	0.985
2		-	0.155	0.204
3			-	0.997
4				-

Root Potassium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.041	0.01	3	3.15	0.086
Error	0.034	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.938	0.107	0.611
2		-	0.237	0.901
3			-	0.539
4				-

Shoot Total Cation Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.085	0.03	3	1.85	0.216
Error	0.122	0.02	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.398	0.991	0.870
2		-	0.276	0.806
3			-	0.724
4				-

Appendix 4 (continued): Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions.

One-way Analysis of Variance

Root Total Cation Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.165	0.05	3	4.02	0.051
Error	0.109	0.01	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.938	0.074	0.358
2		-	0.168	0.656
3			-	0.672
4				-

Analysis of variance for simple linear regressions

Source of variation	DF	SS	MS	F
[Ca] in solution vs. [Ca] in shoots				
Due to regression (R)	1	0.03943	0.03943	10.85*
Deviation about regression (D)	10	0.03633	0.00363	
[Ca] in solution vs. [Ca] in roots				
R	1	0.00248	0.00248	18.38*
D	10	0.00135	0.00013	
[Mg] in solution vs. [Mg] in shoots				
R	1	0.01520	0.01520	4.93*
D	10	0.03086	0.00309	
[Mg] in solution vs. [Mg] in roots				
R	1	0.01415	0.01415	16.46*
D	10	0.00860	0.00086	
Mg/Ca in solution vs. [Ca] in shoots				
R	1	0.02879	0.02879	6.13*
D	10	0.04698	0.00470	
Mg/Ca in solution vs. [Ca] in roots				
R	1	0.00220	0.00220	13.48*
D	10	0.00163	0.00016	
Mg/Ca in solution vs. [Mg] in shoots				
R	1	0.00650	0.00650	1.64
D	10	0.03955	0.00396	

Appendix 4 (continued): Experiment 1 cation concentrations; raw data, one-way analyses of variance, and linear regressions.

Analysis of variance for simple linear regressions (continued)

Source of variation	DF	SS	MS	F
Mg/Ca in solution vs. [Mg] in roots				
R	1	0.00982	0.00982	7.59*
D	10	0.01293	0.00129	
Mg/Ca in solution vs. [Na] in shoots				
R	1	0.00008	0.00008	0.04
D	10	0.02115	0.00212	
Mg/Ca in solution vs. [Na] in roots				
R	1	0.00917	0.00917	3.15
D	10	0.02917	0.00292	
Mg/Ca in solution vs. [K] in shoots				
R	1	0.00499	0.00499	1.33
D	10	0.03738	0.00374	
Mg/Ca in solution vs. [K] in roots				
R	1	0.00905	0.00905	1.38
D	10	0.06578	0.00658	
Mg/Ca in solution vs. [TC] in shoots				
R	1	0.00008	0.00008	0.004
D	10	0.20714	0.02071	
Mg/Ca in solution vs. [TC] in roots				
R	1	0.05910	0.05910	2.75
D	10	0.21507	0.02151	

F must be greater than 4.96 for significance at P less than 0.05

Appendix 5: Experiment 1 cation ratios; raw data , one-way analyses of variance, and linear regressions.

Raw Data, Means and SEM

Treatment	Mg/Ca S	Mg/Ca R	Na/TC S	Na/TC R	Mg/TC S	Mg/TC R
1	0.88	1.65	0.21	0.30	0.13	0.15
	1.12	1.97	0.18	0.25	0.20	0.24
	0.61	2.64	0.15	0.24	0.20	0.23
	0.87	2.09	0.18	0.26	0.18	0.21
	± 0.15	± 0.29	± 0.02	± 0.02	± 0.03	± 0.03
2	2.13	4.29	0.24	0.34	0.23	0.23
	1.69	4.19	0.17	0.23	0.26	0.21
	1.45	2.46	0.14	0.24	0.28	0.21
	1.76	3.65	0.18	0.27	0.26	0.22
	± 0.20	± 0.59	± 0.03	± 0.04	± 0.02	± 0.01
3	2.51	5.00	0.21	0.29	0.31	0.20
	2.59	4.72	0.12	0.27	0.26	0.24
	2.66	4.98	0.18	0.24	0.29	0.27
	2.59	4.90	0.17	0.26	0.29	0.23
	± 0.04	± 0.09	± 0.03	± 0.01	± 0.01	± 0.02
4	3.04	6.82	0.19	0.26	0.25	0.25
	4.03	6.44	0.20	0.32	0.31	0.24
	3.33	7.14	0.18	0.30	0.24	0.25
	3.47	6.80	0.19	0.29	0.26	0.24
	± 0.29	± 0.20	± 0.01	± 0.02	± 0.02	± 0.00

Appendix 5 (continued): Experiment 1 cation ratios; raw data, one-way analyses of variance. and linear regressions.

Raw Data, Means and SEM

Treatment	Ca/TC S	Ca/TC R	K/TC S	K/TC R
1	0.15	0.09	0.52	0.45
	0.18	0.12	0.43	0.39
	0.33	0.09	0.33	0.45
	0.22	0.10	0.42	0.43
	± 0.05	± 0.01	± 0.07	± 0.02
2	0.11	0.05	0.42	0.37
	0.15	0.05	0.42	0.50
	0.20	0.09	0.38	0.46
	0.15	0.06	0.41	0.45
	± 0.03	± 0.01	± 0.02	± 0.04
3	0.12	0.04	0.37	0.48
	0.10	0.05	0.52	0.45
	0.11	0.05	0.42	0.44
	0.11	0.05	0.44	0.46
	± 0.01	± 0.00	± 0.05	± 0.01
4	0.08	0.04	0.48	0.46
	0.08	0.04	0.42	0.41
	0.07	0.04	0.51	0.42
	0.08	0.04	0.47	0.43
	± 0.00	± 0.00	± 0.03	± 0.02

Appendix 5 (continued): Experiment 1 cation ratios; raw data, one-way analyses of variance, and linear regressions.

One-way Analysis of Variance

Shoot Mg/Ca Ratio

Source of variation	SS	MS	DF	F	P
Groups	11.10	3.72	3	33.13	0.000*
Error	0.90	0.11	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.069	0.002*	0.000*
2		-	0.091	0.002*
3			-	0.072
4				-

Root Mg/Ca Ratio

Source of variation	SS	MS	DF	F	P
Groups	35.80	11.90	3	32.64	0.000*
Error	2.92	0.37	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.077	0.003*	0.000*
2		-	0.172	0.002*
3			-	0.032*
4				-

Shoot Na/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.001	0.00	3	0.14	0.932
Error	0.011	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	1.000	0.990	0.991
2		-	0.982	0.996
3			-	0.934
4				-

Appendix 5 (continued): Experiment 1 cation ratios; raw data, one-way analyses of variance, and linear regressions.

One-way Analysis of Variance

Root Na/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.002	0.00	3	0.38	0.771
Error	0.013	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.992	1.000	0.821
2		-	0.996	0.934
3			-	0.851
4				-

Shoot Mg/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.020	0.01	3	5.95	0.020*
Error	0.009	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.102	0.029*	0.077
2		-	0.811	0.997
3			-	0.898
4				-

Root Mg/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.002	0.00	3	0.88	0.492
Error	0.007	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.982	0.781	0.556
2		-	0.936	0.762
3			-	0.976
4				-

Appendix 5 (continued): Experiment 1 cation ratios; raw data, one-way analyses of variance, and linear regressions.

One-way Analysis of Variance

Shoot Ca/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.337	0.01	3	3.92	0.054
Error	0.229	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.547	0.187	0.069
2		-	0.819	0.437
3			-	0.892
4				-

Root Ca/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.007	0.00	3	11.88	0.003*
Error	0.002	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.070	0.013*	0.004*
2		-	0.633	0.215
3			-	0.792
4				-

Shoot K/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.006	0.00	3	0.46	0.719
Error	0.036	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.992	0.998	0.874
2		-	0.967	0.739
3			-	0.938
4				-

Appendix 5 (continued): Experiment 1 cation ratios; raw data, one-way analyses of variance and linear regressions.

One-way Analysis of Variance

Root K/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.002	0.00	3	0.34	0.800
Error	0.013	0.00	8		

Probability matrix for Scheffe multiple comparison of means

Group	1	2	3	4
1	-	0.968	0.906	0.999
2		-	0.996	0.939
3			-	0.857
4				-

Analysis of variance for simple linear regressions

Source of variation	DF	SS	MS	F
Mg/Ca in solution vs. Mg/Ca in shoots				
Due to regression (R)	1	10.25468	10.25468	57.28*
Deviation about regression (D)	10	1.79012	0.17901	
Mg/Ca in solution vs. Mg/Ca in roots				
R	1	33.82741	33.82741	69.59*
D	10	4.86095	0.48609	
Mg/Ca in solution vs. Ca/TC in shoots				
R	1	0.02767	0.02767	9.59*
D	10	0.02887	0.00289	
Mg/Ca in solution vs. Ca/TC in roots				
R	1	0.00507	0.00507	14.56*
D	10	0.00348	0.00035	
Mg/Ca in solution vs. Na/TC in shoots				
R	1	0.00012	0.00012	0.11
D	10	0.01162	0.00116	
Mg/Ca in solution vs. Na/TC in roots				
R	1	0.00143	0.00143	1.05
D	10	0.01359	0.00136	
Mg/Ca in solution vs. K/TC in shoots				
R	1	0.00533	0.00533	1.43
D	10	0.03732	0.00373	

Appendix 5 (continued): Experiment 1 cation ratios; raw data, one-way analyses of variance and linear regressions.

Analysis of variance for simple linear regressions (continued)

Source of variation	DF	SS	MS	F
Mg/Ca in solution vs K/TC in roots				
R	1	0.00017	0.00017	0.12
D	10	0.01447	0.00145	
Mg/Ca in solution vs. Mg/TC in shoots				
R	1	0.00683	0.00683	3.01
D	10	0.02269	0.00227	
Mg/Ca in solution vs. Mg/TC in roots				
R	1	0.00219	0.00219	2.94
D	10	0.00744	0.00074	

F must be greater than 4.96 for significance at P less than 0.05

Appendix 6: Experiment 1 correlations of dry weight with cation concentrations and ratios.

Shoot or root variables	Correlation of shoot variables with shoot dry weight	Probability r=0	Correlation of root variables with root dry weight	Probability r=0
Shoot height	0.669	0.017*	-	-
Shoot number	0.911	0.000*	-	-
[Ca]	-0.225	0.483	0.004	0.991
[Mg]	-0.433	0.160	-0.770	0.003*
[Na]	0.231	0.470	-0.395	0.204
[K]	0.197	0.539	-0.654	0.021*
[TC]	-0.177	0.583	-0.711	0.010*
Mg/Ca	0.081	0.802	-0.287	0.366
Na/TC	0.520	0.083	0.166	0.606
Mg/TC	-0.426	0.167	-0.366	0.242
Ca/TC	-0.243	0.448	0.260	0.414
K/TC	0.363	0.209	-0.073	0.821

Appendix 7: Experiment 2 growth variables; raw data, one-way and two-way analyses of variance.

Raw Data, Means and SEM

Treatment	# S	S Ht (cm)	% SWC	F Wt S (gm)	D Wt S (gm)	D Wt R (gm)	Succulence (F Wt/D Wt)
A1	32	24	306	6.56	1.62	0.68	4.06
	17	20	293	2.24	0.57	0.39	3.93
	8	17	286	1.22	0.32	0.38	3.86
	43	25	277	6.84	1.81	0.74	3.77
	25	22	291	4.21	1.08	0.55	3.91
	± 8	± 2	± 6	± 1.45	± 0.37	± 0.09	± 0.06
B1	31	25	307	3.82	0.94	0.51	4.07
	22	25	273	3.75	1.01	0.48	3.73
	35	24	302	4.97	1.24	0.71	4.02
	19	20	297	2.28	0.57	0.47	3.97
	27	24	295	3.71	0.94	0.54	3.95
	± 4	± 1	± 8	± 0.55	± 0.14	± 0.06	± 0.08
A2	7	10	243	0.55	0.16	0.23	3.43
	13	22	287	2.13	0.55	0.36	3.87
	25	21	266	3.48	0.95	0.58	3.66
	33	22	267	4.62	1.26	0.62	3.67
	20	19	266	2.70	0.73	0.45	3.66
	± 6	± 3	± 9	± 0.88	± 0.24	± 0.09	± 0.09
B2	22	19	317	2.88	0.69	0.48	4.17
	8	18	218	0.95	0.30	0.45	3.18
	22	21	282	3.81	1.00	0.67	3.82
	9	14	243	0.74	0.22	0.39	3.43
	15	18	265	2.09	0.55	0.50	3.65
	± 4	± 1	± 22	± 0.75	± 0.18	± 0.06	± 0.22
A3	16	18	266	1.74	0.48	0.39	3.66
	17	17	258	2.06	0.57	0.42	3.58
	17	18	262	1.90	0.53	0.40	3.62
	± 1	± 1	± 4	± 0.16	± 0.05	± 0.02	± 0.04
B3	-	-	-	-	0.32	-	-
	-	-	-	-	0.33	-	-
	-	-	-	-	0.36	-	-
	-	-	-	-	0.39	-	-
					0.35		
					± 0.02		
C	6	18	271	0.50	0.13	0.33	3.71
	18	22	279	3.03	0.80	0.32	3.79
	30	22	304	3.87	0.96	0.36	4.04
	38	21	281	5.40	1.42	0.65	3.81
	23	21	284	3.20	0.83	0.42	3.84
	± 7	± 1	± 7	± 1.03	± 0.27	± 0.08	± 0.07

Appendix 7 (continued): Experiment 2 growth variables; raw data, one-way and two-way analyses of variance.

Two-way Analysis of Variance

X = Mg/Ca ratios, Y = salt concentrations

Shoot Dry Weight

Source	SS	MS	DF	F	P
X	0.140	0.140	1	0.75	0.399
Y	1.141	0.570	2	3.06	0.075
XY	0.002	0.001	2	0.01	0.995
E	2.981	0.186	16		

Scheffe's multiple comparisons of Y

Groups	Contrast	F	P
1 2	0.368	1.46	0.262
1 3	0.571	2.80	0.091
2 3	0.203	0.35	0.708

One-way Analysis of Variance

Number of Shoots

Source of variation	SS	MS	DF	F	P
Groups	390	78	5	0.60	0.700
Error	2087	130	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	1.000	0.992	0.910	0.978	1.000
B1		-	0.973	0.837	0.951	0.999
A2			-	0.998	1.000	0.999
B2				-	1.000	0.964
A3					-	0.993
C						-

Shoot Height

Source of variation	SS	MS	DF	F	P
Groups	94	19	5	1.52	0.240
Error	198	12	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.984	0.937	0.844	0.878	1.000
B1		-	0.612	0.461	0.581	0.937
A2			-	1.000	0.999	0.984
B2				-	1.000	0.937
A3					-	0.945
C						-

Appendix 7 (continued): Experiment 2 growth variables; raw data, one-way and two-way analyses of variance.

One-way Analysis of Variance

Shoot Water Content

Source of variation	SS	MS	DF	F	P
Groups	3666	733	5	1.39	0.279
Error	8422	526	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	1.000	0.796	0.776	0.834	0.992
B1		-	0.673	0.650	0.741	0.992
A2			-	1.000	1.000	0.936
B2				-	1.000	0.925
A3					-	0.939
C						-

Shoot Fresh Weight

Source of variation	SS	MS	DF	F	P
Groups	14	2.81	5	0.78	0.577
Error	58	3.59	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	1.000	0.930	0.771	0.843	0.987
B1		-	0.988	0.911	0.938	1.000
A2			-	0.999	0.998	1.000
B2				-	1.000	0.981
A3					-	0.985
C						-

Shoot Dry Weight

Source of variation	SS	MS	DF	F	P
Groups	1.49	0.25	6	1.23	0.334
Error	3.82	0.20	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	1.000	0.973	0.827	0.908	0.530	0.995
B1		-	0.998	0.953	0.976	0.747	1.000
A2			-	0.999	1.000	0.958	1.000
B2				-	1.000	0.999	0.991
A3					-	1.000	0.995
B3						-	0.886
C							-

Appendix 7 (continued): Experiment 2 growth variables; raw data, one-way and two-way analyses of variance.

One-way Analysis of Variance

Root Dry Weight

Source of variation	SS	MS	DF	F	P
Groups	0.066	0.01	5	0.58	0.716
Error	0.367	0.02	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	1.000	0.969	0.999	0.940	0.911
B1		-	0.975	1.000	0.947	0.923
A2			-	0.998	1.000	1.000
B2				-	0.988	0.986
A3					-	1.000
C						-

Succulence

Source of variation	SS	MS	DF	F	P
Groups	0.367	0.07	5	1.39	0.279
Error	0.842	0.05	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	1.000	0.796	0.776	0.834	0.999
B1		-	0.673	0.650	0.741	0.992
A2			-	1.000	1.000	0.936
B2				-	1.000	0.925
A3					-	0.939
C						-

Appendix 8: Barley (Hordeum vulgare) raw data, Experiment 2.

All concentrations are in me/g

Treatment	D Wt S(gm)	D Wt R(gm)	[Ca] S	[Ca] R	[Mg] S	[Mg] R	[Na] S	[Na] R
HA1	0.027	0.015	1.03	0.81	1.92	0.51	3.75	0.81
HB1	0.094	0.023	0.72	1.00	1.59	0.44	2.63	0.96
HA2	0.051	0.022	0.57	0.69	1.58	0.39	3.99	0.50
HB2	0.123	0.028	1.36	1.85	1.24	0.48	2.71	0.78
HA3	0.053	0.024	0.26	0.65	0.20	0.39	1.04	2.26
HB3	0.022	0.020	1.05	3.97	1.11	0.33	6.18	1.19
HC1	8.280	1.618	0.80	0.30	0.23	0.15	0.04	0.12

	[K] S	[K] R	[TC] S	[TC] R	Mg/Ca S	Mg/Ca R	Na/TC S	Na/TC R
HA1	0.57	0.22	7.26	2.34	1.9	0.6	0.52	0.34
HB1	0.77	0.25	5.71	2.64	2.2	0.4	0.46	0.36
HA2	0.25	0.07	6.39	1.66	2.8	0.6	0.62	0.30
HB2	0.47	0.22	5.78	3.33	0.9	0.3	0.47	0.24
HA3	0.07	0.14	1.57	3.44	0.8	0.6	0.66	0.66
HB3	0.30	0.11	8.65	5.61	1.0	0.1	0.72	0.21
HC1	1.07	1.20	2.13	1.77	0.3	0.5	0.02	0.07

	Mg/TC S	Mg/TC R	Ca/TC S	Ca/TC R	K/TC S	K/TC R
HA1	0.26	0.22	0.14	0.34	0.08	0.09
HB1	0.28	0.17	0.13	0.38	0.14	0.09
HA2	0.25	0.24	0.09	0.42	0.04	0.04
HB2	0.21	0.14	0.24	0.55	0.08	0.07
HA3	0.13	0.11	0.17	0.19	0.04	0.04
HB3	0.13	0.06	0.12	0.71	0.04	0.02
HC1	0.11	0.09	0.37	0.17	0.50	0.68

Appendix 9: Experiment 2 pressure bomb raw data, one-way analysis of variance, and correlation test.

Raw Data, Means and SEM

Water potential (-kPa)

Treatment

A1	B1	A2	B2	A3	C
620	720	850	810	1210	550
970	770	660	680	1450	620
910	620	680	840	1160	690
760	590	670	790	1310	340
840	850	990	720	1450	540
720	520	1050	710	1090	670
760	680	970	630	1120	590
620	550	720	640	1120	380
690	670	770	970	1160	370
810	550	860	780	1450	320
770	650	820	760	1250	510
± 37	± 34	± 46	± 33	± 47	± 45

One-way Analysis of Variance

Source of variation	SS	MS	DF	F	P
Groups	315	63	5	38.39	0.000*
Error	88	2	54		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.522	0.974	1.000	0.000*	0.003*
B1		-	0.137	0.647	0.000*	0.286
A2			-	0.934	0.000*	0.000*
B2				-	0.000*	0.005*
A3					-	0.000*
C						-

Correlation between plant water potential and solution water potential

r = 0.858 P that r = 0 is 0.000*

Appendix 10: Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.

Raw Data, Means and SEM
Concentrations in me/g

Treatment	[Ca] S	[Ca] R	[Mg] S	[Mg] R	[Na] S	[Na] R
A1	0.089	0.056	0.199	0.154	0.192	0.185
	0.115	0.103	0.262	0.202	0.182	0.178
	0.143	0.086	0.289	0.219	0.316	0.156
	0.055	0.043	0.130	0.171	0.120	0.155
	0.101	0.072	0.220	0.187	0.203	0.169
	± 0.019	± 0.014	± 0.036	± 0.015	± 0.041	± 0.008
B1	0.360	0.255	0.183	0.188	0.186	0.193
	0.556	0.339	0.186	0.220	0.166	0.140
	0.208	0.201	0.187	0.194	0.154	0.166
	0.147	0.386	0.249	0.208	0.227	0.144
	0.318	0.295	0.201	0.203	0.183	0.161
	± 0.091	± 0.042	± 0.016	± 0.007	± 0.016	± 0.012
A2	0.169	0.120	0.248	0.165	0.429	0.183
	0.086	0.091	0.192	0.168	0.203	0.177
	0.069	0.055	0.179	0.173	0.214	0.212
	0.071	0.059	0.154	0.174	0.165	0.234
	0.099	0.081	0.193	0.170	0.253	0.202
	± 0.024	± 0.015	± 0.020	± 0.002	± 0.060	± 0.013
B2	0.167	0.768	0.184	0.199	0.250	0.215
	0.192	0.377	0.310	0.190	0.231	0.207
	0.194	0.236	0.164	0.198	0.180	0.192
	0.434	0.795	0.207	0.216	0.197	0.162
	0.247	0.544	0.216	0.201	0.215	0.194
	± 0.063	± 0.140	± 0.033	± 0.006	± 0.016	± 0.012
A3	0.072	0.077	0.198	0.205	0.517	0.501
	0.091	0.077	0.166	0.221	0.314	0.632
	0.082	0.077	0.182	0.213	0.416	0.567
	± 0.010	± 0	± 0.016	± 0.008	± 0.102	± 0.066
B3	0.354	-	0.285	-	0.508	-
	0.372	-	0.148	-	0.562	-
	0.989	-	0.445	-	1.453	-
	0.294	-	0.222	-	0.609	-
	0.502		0.275		0.783	
	± 0.163		± 0.063		± 0.224	
C	0.423	0.441	0.246	0.077	0.081	0.030
	0.402	0.199	0.183	0.102	0.039	0.046
	0.273	0.230	0.169	0.077	0.040	0.056
	0.298	0.080	0.137	0.115	0.028	0.030
	0.349	0.238	0.184	0.093	0.047	0.041
	± 0.038	± 0.075	± 0.023	± 0.010	± 0.012	± 0.006

Appendix 10 (continued): Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.

Raw Data, Means and SEM
Concentrations in me/g

Treatment	[K] S	[K] R	[TC] S	[TC] R
A1	0.698	0.399	1.178	0.794
	0.548	0.279	1.107	0.762
	0.610	0.228	1.358	0.689
	0.573	0.413	0.878	0.782
	0.607	0.330	1.130	0.757
	± 0.033	± 0.045	± 0.099	± 0.024
B1	0.568	0.333	1.297	0.969
	0.438	0.381	1.346	1.080
	0.558	0.469	1.107	1.030
	0.550	0.220	1.173	0.958
	0.529	0.351	1.231	1.009
	± 0.030	± 0.052	± 0.055	± 0.028
A2	0.472	0.105	1.318	0.573
	0.547	0.330	1.028	0.766
	0.532	0.305	0.994	0.745
	0.457	0.373	0.847	0.840
	0.502	0.278	1.047	0.731
	± 0.022	± 0.059	± 0.099	± 0.056
B2	0.678	0.270	1.279	1.452
	0.412	0.189	1.145	0.963
	0.610	0.317	1.148	0.943
	0.497	0.122	1.335	1.295
	0.549	0.225	1.227	1.163
	± 0.059	± 0.043	± 0.048	± 0.126
A3	0.468	0.174	1.255	0.957
	0.419	0.207	0.990	1.137
	0.444	0.191	1.123	1.047
	± 0.025	± 0.017	± 0.133	± 0.090
B3	0.035	-	1.182	-
	0.039	-	1.121	-
	0.105	-	2.992	-
	0.037	-	1.162	-
	0.054		1.614	
	± 0.017		± 0.459	
C	0.718	0.101	1.468	0.649
	0.545	0.327	1.169	0.674
	0.723	0.255	1.205	0.618
	0.624	0.469	1.087	0.694
	0.653	0.288	1.232	0.659
	± 0.043	± 0.077	± 0.082	± 0.016

Appendix 10 (continued): Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.

Two-way Analysis of Variance

Shoot Calcium Concentration

Source	SS	MS	DF	F	P
X	0.353	0.353	1	11.83	0.003*
Y	0.046	0.023	2	0.77	0.479
XY	0.062	0.031	2	1.03	0.379
E	0.477	0.030	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	0.036	0.09	0.916
1	3	-0.083	0.37	0.698
2	3	-0.119	0.76	0.483

Shoot Magnesium Concentration

Source	SS	MS	DF	F	P
X	0.005	0.005	1	1.03	0.325
Y	0.002	0.001	2	0.18	0.838
XY	0.010	0.005	2	0.95	0.406
E	0.084	0.005	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	0.006	0.01	0.987
1	3	-0.018	0.10	0.908
2	3	-0.024	0.17	0.844

Shoot Sodium Concentration

Source	SS	MS	DF	F	P
X	0.055	0.055	1	1.27	0.277
Y	0.603	0.301	2	6.95	0.007*
XY	0.157	0.079	2	1.82	0.195
E	0.693	0.043	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	-0.041	0.08	0.927
1	3	-0.406	6.10	0.011*
2	3	-0.366	4.94	0.021

Appendix 10 (continued): Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.

Two-way Analysis of Variance

Shoot Potassium Concentration

Source	SS	MS	DF	F	P
X	0.101	0.101	1	21.22	0.000*
Y	0.362	0.181	2	37.95	0.000*
XY	0.156	0.078	2	16.29	0.000*
E	0.076	0.005	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	0.042	0.75	0.489
1	3	0.319	34.14	0.000*
2	3	0.277	25.70	0.000*

Shoot Total Cation Concentration

Source	SS	MS	DF	F	P
X	0.341	0.341	1	1.90	0.187
Y	0.184	0.092	2	0.51	0.609
XY	0.130	0.065	2	0.36	0.702
E	2.867	0.179	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	0.044	0.02	0.979
1	3	-0.188	0.32	0.734
2	3	-0.232	0.48	0.628

One-way Analysis of Variance

Shoot Calcium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.549	0.09	6	3.52	0.016*
Error	0.494	0.03	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	0.723	1.000	0.942	1.000	0.106	0.588
B1		-	0.716	0.999	0.817	0.845	1.000
A2			-	0.939	1.000	0.103	0.580
B2				-	0.960	0.557	0.990
A3					-	0.227	0.718
B3						-	0.929
C							-

Appendix 10 (continued): Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

Root Calcium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.647	0.13	5	6.28	0.002*
Error	0.329	0.02	16		

F ratios matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	4.83	0.01	21.65*	0.00	2.65
B1		-	4.45	6.03	3.08	0.33
A2			-	20.83*	0.00	2.37
B2				-	14.12	9.16
A3					-	1.66
C						-

F must be greater than 14.25 for significance at $p < 0.05$

Shoot Magnesium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.023	0.00	6	0.81	0.575
Error	0.090	0.00	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	1.000	0.999	1.000	0.999	0.968	0.996
B1		-	1.000	1.000	1.000	0.882	1.000
A2			-	1.000	1.000	0.823	1.000
B2				-	0.999	0.957	0.998
A3					-	0.867	1.000
B3						-	0.739
C							-

Root Magnesium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.036	0.01	5	24.02	0.000*
Error	0.005	0.00	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.882	0.868	0.923	0.686	0.000*
B1		-	0.277	1.000	0.991	0.000*
A2			-	0.331	0.208	0.001*
B2				-	0.983	0.000*
A3					-	0.000*
C						-

Appendix 10 (continued): Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

Shoot Sodium Concentration

Source of variation	SS	MS	DF	F	P
Groups	1.344	0.22	6	6.13	0.001*
Error	0.695	0.04	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	1.000	1.000	1.000	0.942	0.028*	0.965
B1		-	1.000	1.000	0.914	0.022*	0.982
A2			-	1.000	0.984	0.055	0.879
B2				-	0.955	0.033*	0.951
A3					-	0.568	0.565
B3						-	0.003*
C							-

Root Sodium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.379	0.08	5	79.22	0.000*
Error	0.015	0.00	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	1.000	0.803	0.922	0.000*	0.001*
B1		-	0.635	0.798	0.000*	0.003*
A2			-	1.000	0.000*	0.000*
B2				-	0.000*	0.000*
A3					-	0.000*
C						-

Shoot Potassium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.943	0.16	6	30.47	0.000*
Error	0.098	0.01	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	0.869	0.642	0.967	0.370	0.000*	0.991
B1		-	1.000	1.000	0.923	0.000*	0.458
A2			-	0.988	0.987	0.000*	0.243
B2				-	0.814	0.000*	0.661
A3					-	0.001*	0.137
B3						-	0.000*
C							-

Appendix 10 (continued): Experiment 2 cation concentrations; raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

Root Potassium Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.058	0.01	5	0.96	0.469
Error	0.193	0.01	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	1.000	0.993	0.863	0.822	0.997
B1		-	0.968	0.751	0.723	0.983
A2			-	0.992	0.970	1.000
B2				-	1.000	0.982
A3					-	0.953
C						-

Shoot Total Cation Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.787	0.13	6	0.84	0.551
Error	2.948	0.16	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	1.000	1.000	1.000	1.000	0.798	1.000
B1		-	0.998	1.000	1.000	0.921	1.000
A2			-	0.998	1.000	0.659	0.998
B2				-	1.000	0.917	1.000
A3					-	0.903	1.000
B3						-	1.000
C							-

Root Total Cation Concentration

Source of variation	SS	MS	DF	F	P
Groups	0.789	0.16	5	9.58	0.000*
Error	0.263	0.02	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.231	1.000	0.015*	0.289	0.942
B1		-	0.154	0.718	1.000	0.043*
A2			-	0.009*	0.212	0.984
B2				-	0.949	0.002*
A3					-	0.079
C						-

Appendix 11: Experiment 2 cation ratios; raw data, two-way and one-way analyses of variance.

Raw Data, Means and SEM

Treatment	Mg/Ca	Mg/Ca	Na/TC	Na/TC	Mg/TC	Mg/TC
	S	R	S	R	S	R
A1	2.20	2.75	0.16	0.23	0.17	0.19
	2.30	2.00	0.16	0.23	0.24	0.27
	2.00	2.50	0.23	0.23	0.21	0.32
	2.40	4.00	0.14	0.20	0.15	0.22
	2.23	2.81	0.17	0.22	0.19	0.25
B1	0.51	0.74	0.14	0.20	0.14	0.19
	0.33	0.65	0.12	0.13	0.14	0.20
	0.90	0.97	0.14	0.16	0.17	0.19
	1.70	0.54	0.19	0.15	0.21	0.22
	0.86	0.73	0.15	0.16	0.17	0.20
	± 0.30	± 0.09	± 0.02	± 0.02	± 0.02	± 0.01
A2	1.50	1.40	0.33	0.32	0.19	0.29
	2.20	1.80	0.20	0.23	0.19	0.22
	2.60	3.10	0.22	0.28	0.18	0.23
	2.20	2.90	0.19	0.28	0.18	0.21
	2.13	2.30	0.24	0.28	0.18	0.24
	± 0.23	± 0.41	± 0.03	± 0.02	± 0.00	± 0.02
B2	1.10	0.26	0.20	0.15	0.14	0.14
	1.60	0.50	0.20	0.21	0.27	0.20
	0.85	0.84	0.16	0.20	0.14	0.21
	0.48	0.27	0.15	0.13	0.16	0.17
	1.01	0.47	0.18	0.17	0.18	0.18
	± 0.24	± 0.14	± 0.01	± 0.02	± 0.03	± 0.02
A3	2.75	2.70	0.41	0.52	0.16	0.21
	1.80	2.90	0.32	0.56	0.17	0.19
	2.28	2.80	0.37	0.54	0.16	0.20
	± 0.48	± 0.10	± 0.05	± 0.02	± 0.01	± 0.01
B3	0.81	-	0.43	-	0.24	-
	0.40	-	0.50	-	0.13	-
	0.45	-	0.49	-	0.15	
	0.76	-	0.52	-	0.19	-
	0.61		0.49		0.18	
	± 0.11		± 0.02		± 0.02	
C	0.58	0.17	0.06	0.05	0.17	0.12
	0.46	0.51	0.03	0.07	0.16	0.15
	0.62	0.33	0.03	0.09	0.14	0.12
	0.46	1.40	0.03	0.04	0.13	0.17
	0.53	0.60	0.04	0.06	0.15	0.14
	± 0.04	± 0.28	± 0.01	± 0.01	± 0.01	± 0.01

Appendix 11 (continued): Experiment 2 cation ratios; raw data,
two-way and one-way analyses of variance.

Raw Data, Means and SEM

Treatment	Ca/TC S	Ca/TC R	K/TC S	K/TC R
A1	0.08	0.07	0.59	0.50
	0.10	0.14	0.50	0.37
	0.11	0.12	0.45	0.33
	0.06	0.05	0.65	0.53
	0.09	0.10	0.55	0.43
	± 0.01	± 0.02	± 0.05	± 0.05
B1	0.28	0.26	0.44	0.34
	0.41	0.31	0.33	0.35
	0.19	0.20	0.50	0.46
	0.13	0.40	0.47	0.23
	0.25	0.29	0.44	0.35
	± 0.06	± 0.04	± 0.04	± 0.05
A2	0.13	0.21	0.36	0.18
	0.08	0.12	0.53	0.43
	0.07	0.07	0.54	0.41
	0.08	0.07	0.54	0.44
	0.09	0.12	0.49	0.37
	± 0.01	± 0.03	± 0.04	± 0.06
B2	0.13	0.53	0.53	0.19
	0.17	0.39	0.36	0.20
	0.17	0.25	0.53	0.34
	0.33	0.61	0.37	0.09
	0.20	0.45	0.45	0.21
	± 0.04	± 0.08	± 0.05	± 0.05
A3	0.06	0.08	0.37	0.18
	0.09	0.07	0.42	0.18
	0.08	0.08	0.40	0.18
	± 0.02	± 0.01	± 0.03	± 0
B3	0.30	-	0.03	-
	0.33	-	0.03	-
	0.33	-	0.04	-
	0.25	-	0.03	-
	0.30		0.03	
	± 0.02		± 0.00	
C	0.29	0.68	0.49	0.16
	0.34	0.30	0.47	0.49
	0.23	0.37	0.60	0.41
	0.27	0.12	0.57	0.68
	0.28	0.37	0.53	0.44
	± 0.02	± 0.12	± 0.03	± 0.11

Appendix 11 (continued): Experiment 2 cation ratios; raw data, two-way and one-way analyses of variance.

Two-way Analysis of Variance

Shoot Mg/Ca Ratio

Source	SS	MS	DF	F	P
X	9.853	9.853	1	51.33	0.000*
Y	0.055	0.027	2	0.14	0.869
XY	0.245	0.123	2	0.64	0.541
E	3.072	0.192	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	-0.024	0.01	0.994
1	3	0.102	0.09	0.917
2	3	0.126	0.13	0.876

Shoot Na/TC Ratio

Source	SS	MS	DF	F	P
X	0.001	0.001	1	0.42	0.525
Y	0.243	0.121	2	63.68	0.000*
XY	0.027	0.014	2	7.10	0.006*
E	0.030	0.002	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	-0.046	2.25	0.138
1	3	-0.265	58.99	0.000*
2	3	-0.219	40.20	0.000*

Shoot Mg/TC Ratio

Source	SS	MS	DF	F	P
X	0.000	0.000	1	0.10	0.752
Y	0.000	0.000	2	0.11	0.897
XY	0.000	0.001	2	0.42	0.664
E	0.027	0.002	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	-0.003	0.01	0.990
1	3	0.008	0.06	0.945
2	3	0.011	0.11	0.900

Appendix 11 (continued): Experiment 2 cation ratios; raw data, two-way and one-way analyses of variance.

Two-way Analysis of Variance

Shoot Ca/TC Ratio

Source	SS	MS	DF	F	P
X	0.144	0.144	1	30.19	0.000*
Y	0.006	0.003	2	0.67	0.525
XY	0.011	0.006	2	1.16	0.337
E	0.076	0.005	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	0.025	0.26	0.773
1	3	-0.019	0.12	0.890
2	3	-0.044	0.64	0.540

Shoot K/TC Ratio

Source	SS	MS	DF	F	P
X	0.155	0.155	1	26.68	0.000*
Y	0.287	0.143	2	24.75	0.000*
XY	0.085	0.043	2	7.35	0.005*
E	0.093	0.006	16		

Scheffe's multiple comparisons of Y

Groups		Contrast	F	P
1	2	0.021	0.16	0.857
1	3	0.277	21.28	0.000*
2	3	0.256	18.14	0.000*

One-way Analysis of Variance

Shoot Mg/Ca Ratio

Source of variation	SS	MS	DF	F	P
Groups	13.47	2.24	6	13.79	0.000*
Error	3.09	0.16	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	0.012*	1.000	0.030*	1.000	0.002*	0.001*
B1		-	0.022*	1.000	0.044*	0.990	0.964
A2			-	0.055	1.000	0.004*	0.003*
B2				-	0.089	0.912	0.824
A3					-	0.012*	0.008*
B3						-	1.000
C							-

Appendix 11 (continued): Experiment 2 cation ratios; raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

Root Mg/Ca Ratio

Source of variation	SS	MS	DF	F	P
Groups	22.72	4.54	5	13.27	0.000*
Error	5.48	0.34	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.006*	0.902	0.002*	1.000	0.003*
B1		-	0.048*	0.995	0.029*	1.000
A2			-	0.016*	0.960	0.029*
B2				-	0.012*	1.000
A3					-	0.019*
C						-

Shoot Na/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.494	0.08	6	50.25	0.000*
Error	0.031	0.00	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	0.991	0.586	1.000	0.003*	0.000*	0.013*
B1		-	0.214	0.978	0.001*	0.000*	0.062
A2			-	0.673	0.078*	0.000*	0.000*
B2				-	0.004*	0.000*	0.010*
A3					-	0.124	0.000*
B3						-	0.000*
C							-

Root Na/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.339	0.07	5	76.98	0.000*
Error	0.014	0.00	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.176	0.286	0.382	0.000*	0.000*
B1		-	0.002*	0.996	0.000*	0.011*
A2			-	0.006*	0.000*	0.000*
B2				-	0.000*	0.004*
A3					-	0.000*
C						-

Appendix 11 (continued): Experiment 2 cation ratios; raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

Shoot Mg/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.005	0.00	6	0.58	0.745
Error	0.028	0.00	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	0.984	1.000	1.000	0.992	1.000	0.847
B1		-	0.997	1.000	1.000	1.000	0.999
A2			-	1.000	0.999	1.000	0.930
B2				-	1.000	1.000	0.970
A3					-	1.000	1.000
B3						-	0.970
C							-

Root Mg/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.031	0.01	5	5.52	0.004*
Error	0.018	0.00	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.553	0.998	0.172	0.789	0.013*
B1		-	0.807	0.964	1.000	0.312
A2			-	0.346	0.935	0.031*
B2				-	0.973	0.770
A3					-	0.469
C						-

Shoot Ca/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.209	0.03	6	8.00	0.000*
Error	0.083	0.00	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	0.104	1.000	0.472	1.000	0.016*	0.035*
B1		-	0.113	0.969	0.199	0.976	0.998
A2			-	0.499	1.000	0.018*	0.038*
B2				-	0.584	0.579	0.785
A3					-	0.049*	0.089
B3						-	1.000
C							-

Appendix 11 (continued): Experiment 2 cation ratios; raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

Root Ca/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.442	0.09	5	5.07	0.006*
Error	0.279	0.02	16		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.508	1.000	0.052	1.000	0.191
B1		-	0.630	0.748	0.615	0.984
A2			-	0.078	1.000	0.265
B2				-	0.119	0.981
A3					-	0.309
C						-

Shoot K/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.741	0.12	6	22.50	0.000*
Error	0.104	0.01	19		

Probability matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	B3	C
A1	-	0.604	0.978	0.722	0.489	0.000*	1.000
B1		-	0.972	1.000	0.999	0.000*	0.744
A2			-	0.992	0.880	0.000*	0.996
B2				-	0.994	0.000*	0.844
A3					-	0.002*	0.606
B3						-	0.000*
C							-

Root K/TC Ratio

Source of variation	SS	MS	DF	F	P
Groups	0.197	0.039	5	2.32	0.092
Error	0.272	0.017	16		

F ratios matrix for Scheffe multiple comparison of means

Group	A1	B1	A2	B2	A3	C
A1	-	0.89	0.53	6.06	4.98	0.00
B1		-	0.05	2.31	2.14	0.95
A2			-	3.01	2.68	0.58
B2				-	0.05	0.22
A3					-	5.10
C						-

F must be greater than 14.25 to be significant at $p < 0.05$

Appendix 12: Experiment 2 correlations of dry weight with cation concentrations and ratios.

Shoot or root variables	Correlation of shoot variables with shoot dry weight	Probability r = 0	Correlation of root variables with root dry weight	Probability r = 0
[Ca]	-0.293	0.146	-0.217	0.332
[Mg]	-0.574	0.002*	0.132	0.559
[Na]	-0.428	0.029*	-0.043	0.849
[K]	0.417	0.034*	0.773	0.000*
[TC]	-0.351	0.079	0.168	0.455
Mg/Ca	0.188	0.358	0.355	0.105
Na/TC	-0.487	0.012*	-0.107	0.637
Mg/TC	-0.400	0.043*	-0.074	0.744
Ca/TC	-0.248	0.222	-0.378	0.083
K/TC	0.601	0.001*	0.582	0.005*

Appendix 13: Germination raw data, two-way and one-way analyses of variance.

Raw Data, Means and SEM
Number of seeds germinated per dish (total possible = 20)

Osmoticum	Water potential (-kPa)				
	0	-200	-500	-1000	-2000
Na_2SO_4	9	11	6	2	0
	12	5	8	3	0
	10	8	5	2	0
	6	9	5	2	0
	9	10	4	2	0
	9.2	8.6	5.6	2.2	0
	± 1.0	± 1.0	± 0.7	± 0.2	± 0
$MgSO_4$	12	9	3	1	0
	7	9	3	0	0
	8	7	3	0	0
	12	5	2	2	0
	13	5	1	1	0
	10.4	7.0	2.4	0.8	0
	± 1.2	± 0.9	± 0.4	± 0.4	± 0
NaCl	11	9	7	1	0
	5	12	5	3	0
	13	12	6	3	0
	10	7	5	5	0
	10	11	6	4	0
	9.8	10.2	5.8	3.2	0
	± 1.3	± 1.0	± 0.4	± 0.7	± 0
PEG	6	11	1	1	0
	12	6	0	0	0
	5	7	1	0	0
	15	9	0	0	0
	6	11	2	0	0
	8.8	8.8	0.8	0.2	0
	± 2.0	± 1.0	± 0.4	± 0.2	± 0

Appendix 13 (continued): Germination raw data, two-way and one-way analyses of variance.

Two-way Analysis of Variance

A = type of salt B = water potentials

Source	SS	MS	DF	F	P
A	67	22	3	6.63	0.000*
B	1439	360	4	106.72	0.000*
AB	84	7	12	2.08	0.027*
E	270	3	80		

Scheffe's multiple comparisons of A
1 = Na_2SO_4 2 = $MgSO_4$ 3 = NaCl 4 = PEG

Groups		Contrast	F	P
1	2	1.00	1.24	0.302
1	3	-0.68	0.57	0.635
1	4	1.40	2.42	0.072
2	3	-1.68	3.49	0.019*
2	4	0.40	0.20	0.898
3	4	2.08	5.35	0.002*

Scheffe's multiple comparisons of B
1 = 0 kPa 2 = -200 kPa 3 = -500 kPa 4 = -1000 kPa 5 = -2000 kPa

Groups		Contrast	F	P
1	2	0.90	0.60	0.663
1	3	5.90	25.82	0.000*
1	4	7.95	46.89	0.000*
1	5	9.55	67.66	0.000*
2	3	5.00	18.55	0.000*
2	4	7.05	36.87	0.000*
2	5	8.65	55.51	0.000*
3	4	2.05	3.12	0.019*
3	5	3.65	9.88	0.000*
4	5	1.60	1.90	0.119

Appendix 13 (continued): Germination raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

All Salts at 0 kPa

Source of variation	SS	MS	DF	F	P
Groups	7.35	2.45	3	0.24	0.865
Error	161.60	10.10	16		

Probability matrix for Scheffe multiple comparison of means

Group	Na_2SO_4	$MgSO_4$	NaCl	PEG
Na_2SO_4	-	0.948	0.993	0.998
$MgSO_4$		-	0.993	0.887
NaCl			-	0.969
PEG				-

All Salts at -200 kPa

Source of variation	SS	MS	DF	F	P
Groups	25.75	8.58	3	1.79	0.190
Error	76.80	4.80	16		

Probability matrix for Scheffe multiple comparison of means

Group	Na_2SO_4	$MgSO_4$	NaCl	PEG
Na_2SO_4	-	0.725	0.725	0.999
$MgSO_4$		-	0.192	0.648
NaCl			-	0.797
PEG				-

All Salts at -500 kPa

Source of variation	SS	MS	DF	F	P
Groups	90.55	30.18	3	26.83	0.000*
Error	18.00	1.13	16		

Probability matrix for Scheffe multiple comparison of means

Group	Na_2SO_4	$MgSO_4$	NaCl	PEG
Na_2SO_4	-	0.002*	0.993	0.000*
$MgSO_4$		-	0.001*	0.171
NaCl			-	0.000*

All Salts at -1000 kPa

Source of variation	SS	MS	DF	F	P
Groups	27.60	9.20	3	11.15	0.000*
Error	13.20	0.83	16		

Probability matrix for Scheffe multiple comparison of means

Group	Na_2SO_4	$MgSO_4$	NaCl	PEG
Na_2SO_4	-	0.157	0.414	0.026*
$MgSO_4$		-	0.007*	0.780
NaCl			-	0.001*
PEG				-

Appendix 13 (continued): Germination raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

Na_2SO_4 at All Water Potentials

Source of variation	SS	MS	DF	F	P
Groups	319	79.7	4	31.86	0.000*
Error	50	2.5	20		

F ratios matrix for Scheffe multiple comparison of means

Group	0	-200	-500	-1000	-2000
0	-	0.36	12.96*	49.00*	84.64*
-200		-	9.00	40.96*	73.96*
-500			-	11.56*	31.36*
-1000				-	4.84
-2000					-

F must be greater than 11.48 to be significant at $p < 0.05$

$MgSO_4$ at All Water Potentials

Source of variation	SS	MS	DF	F	P
Groups	393	98.4	4	38.42	0.000*
Error	51	2.6	20		

F ratios matrix for Scheffe multiple comparison of means

Group	0	-200	-500	-1000	-2000
0	-	11.29	62.50*	90.00*	106.62*
-200		-	20.76*	37.54*	47.85*
-500			-	2.50	5.63
-1000				-	0.63
-2000					-

F must be greater than 11.48 to be significant at $p < 0.05$

NaCl at All Water Potentials

Source of variation	SS	MS	DF	F	P
Groups	379	94.7	4	29.05	0.000*
Error	65	3.3	20		

F ratios matrix for Scheffe multiple comparison of means

Group	0	-200	-500	-1000	-2000
0	-	0.12	12.27*	33.40*	73.65*
-200		-	14.85*	37.58*	79.79*
-500			-	5.18	25.80*
-1000				-	7.85
-2000					-

F must be greater than 11.48 to be significant at $p < 0.05$

Appendix 13 (continued): Germination raw data, two-way and one-way analyses of variance.

One-way Analysis of Variance

PEG at All Water Potentials

Source of variation	SS	MS	DF	F	P
Groups	432	108	4	20.92	0.000*
Error	103	5	20		

F ratios matrix for Scheffe multiple comparison of means

Group	0	-200	-500	-1000	-2000
0	-	0	31.01*	35.83*	37.52*
-200		-	31.01*	35.83*	37.52*
-500			-	0.17	0.31
-1000				-	0.02
-2000					-

F must be greater than 11.48 to be significant at $p < 0.05$